THE UNIVERSITY OF KANSAS
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ARTICLE 56 (BRYOZOA 2)

RHABDOMESID BRYOZOANS OF THE WREFORD MEGACYCLOTHEM (WOLFCAMPIAN, PERMIAN) OF NEBRASKA, KANSAS, AND OKLAHOMA

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TABLES

TABLE — PAGE

1. Stratigraphic units in the Lower Permian of Kansas and Nebraska; Oklahoma nomenclature (after BRANSON, 1960) appears in parentheses 12
2. Comparison between two observers, collecting bryozoans from material weathering free at the same locality and horizons, and the two observers picking bryozoans from a post-kerosene-treatment, uncontaminated fresh shale sample from the horizon and locality 18
3. Vertical distribution of bryozoan zoarial growth forms within the upper Havensville calcareous shale at locality MS06. Fresh samples from the upper, middle, and lower thirds of the 3-foot-thick rock unit were collected separately, processed identically, and then completely picked for bryozoans 18
4. Phylogeny of rhabdomesid cryptostomes 25
5. Character-state coding for the two-state analysis of the Rhabdomesidae, as used in the cluster analysis of its component genera 26
6. Summary of two-state coding for genera of the Rhabdomesidae, as used for the cluster analysis of those genera 27
7. Summary of measurements made on Wreford specimens of *Rhombopora lepidodendroides* MEEK, 1872 31
8. Summary of measurements made on Wreford specimens of *Syringoclemis wrefordensis* NEWTON, n. sp. 36
9. Classification of numerical morphological characteristics into four groups based upon coefficients of variation (CV) computed for *Rhombopora lepidodendroides* 40
10. Classification of numerical morphological characteristics into four groups based upon coefficients of variation (CV) computed for *Syringoclemis wrefordensis* 40

THE UNIVERSITY OF KANSAS PALEONTOLOGICAL CONTRIBUTIONS
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CONTENTS

	PAGE
ABSTRACT	5
INTRODUCTION	5
Purpose of study	5
Acknowledgments	6
STRATIGRAPHIC AND PALEONTOLOGIC BACKGROUND FOR WREFORD INVESTIGATIONS	7
Historical summary	7
New observations on important Wreford lithologies	7
New observations on stratigraphy of the Wreford in Kansas	10
Stratigraphy of the Wreford in Nebraska	13
Stratigraphy of the Wreford in Oklahoma	13
Wreford Megacyclothem locality register	15
Zoarial growth forms	16
METHODS OF STUDY	17
Collection methods	17
Sampling methods	18
Processing of samples	19
Sample sorting techniques	19
Specimen preparation methods	19
Symbolization of morphological parameters	21
Specimen-label symbolization	22
Analysis of data	22
General considerations	22
Statistical treatment method	22
Cluster analysis	23
SYSTEMATIC ANALYSIS OF WREFORD RHABDOMESIDAE	23
Phyla	23
Orders	23
Cryptostome families	24
Family Rhabdomesidae	25
Rhabdomesid generic concepts applicable to Wreford Bryozoa	27
Synonymy and stratigraphic range of *Rhombopora lepidodendroides*	28
New species *Syringoclemis wrefordensis*	29
SKELETAL MORPHOLOGY OF THE WREFORD RHABDOMESIDAE	31
Skeletal morphology of *Rhombopora lepidodendroides*	31
General orientation of colony	31
Wall structure	31
Acanthopores	32
Hemisepta	33
Diaphragms	34
Basal laminae	34
Mesopores	35
Missing skeletal elements	35
Skeletal morphology of *Syringoclemis wrefordensis*	35
General comments	35
Wall structure	35
Acanthopores	36
Hemisepta	36
Diaphragms	36
Basal laminae	37
Mesopores	37
Missing skeletal elements	37
Soft-part morphology of the Wreford Rhabdomesidae	37
VARIABILITY AMONG WREFORD RHABDOMESIDAE	39
Variability, stable taxonomic classification, and numerical analysis	39
Clinal and evolutionary variability	43
PALEOECOLOGY OF WREFORD RHABDOMESIDAE	43
Worldwide paleozoogeography of Late Paleozoic Rhabdomesidae	43
North American and Wreford paleozoogeography of Late Paleozoic Rhabdomesidae	45
Observations on paleoecology of the Wreford Rhabdomesidae	46
SUMMARY AND CONCLUSIONS	47

PAGE

REFERENCES 48
APPENDIX A 52
APPENDIX B 64
APPENDIX C 65

ILLUSTRATIONS

FIGURE PAGE

1. Composite generalized north-south cross section of the Wreford Megacyclothem in southern Nebraska, Kansas, and northern Oklahoma 8-9
2. Outcrop of Wreford Limestone (Lower Permian) in Nebraska, Kansas, and Oklahoma (adapted from Geologic Bedrock of Southeastern Nebraska, 1966; Geologic Map of Kansas, 1964; and Geologic Map of Oklahoma, 1964) 11
3. Wreford localities in southern Nebraska (separately numbered in counties) 15
4. Wreford localities, additional to those of CUFFEY (1966, 1967) in Kansas (separately numbered in counties) 15
5. Wreford localities in northern Oklahoma (separately numbered in counties) 16
6. Step-wise explanation of the specimen embedding technique employed in the preparation of thin sections and peels 20
7. Morphological features and their symbolization used in the assessment of the Wreford Rhabdomesidae 21
8. Dendrogram of the genera of the family Rhabdomesidae based on seven classificatory characters used by BASSLER (1953) 26
9. Dendrogram of the Wreford Rhabdomesidae based on two-state coding of the numerical morphological characteristics 30
10. Reconstruction of the mature rhabdomesid zooid in its extended state (upper zooid) and retracted state (lower zooid) with their relationships to the zooecial wall regions 32
11. Reconstruction of a typical growing tip of a rhabdomesid cryptostome showing soft-part relationships to zooecial wall regions 33
12. Frequency distributions computed from all observations on the characters Z2 and NMA made on the Wreford Megacyclothem specimens of *Rhombopora lepidodendroides* and *Syringoclemis wrefordensis* 41
13. Frequency distributions computed from all observations on the characters Z1 and MMAW made on the Wreford Megacyclothem specimens of *Rhombopora lepidodendroides* and *Syringoclemis wrefordensis* 41
14. Clinal (geographic) variation in the means of MMUW and MZAD for specimens of *Rhombopora lepidodendroides* collected from the middle Threemile and upper Speiser from localities in Nebraska, Kansas, and Oklahoma 42
15. Microevolutionary (stratigraphic) variations in the means of four characters (Z1, MZAD, MMAW, MMUW) shown in specimens of *Rhombopora lepidodendroides* collected from the five widespread Wreford Megacyclothem calcareous shales 43
16. Paleozoogeographic distribution of the family Rhabdomesidae in the United States in the Carboniferous and Permian 44
17. Worldwide paleozoogeographic distribution of the Rhabdomesidae in the Carboniferous and Permian 44
18. Distribution of upper Paleozoic marine rocks in North America 45
19. Distribution of *Syringoclemis wrefordensis* in the uppermost Speiser calcareous shale. Percentages are of total occurrence in the upper Speiser only 46

PLATE FOLLOWING PAGE 71

1. *Rhombopora* (Fig. 1-6, 11, 12), *Syringoclemis* (Fig. 7-10, 13-15)
2. *Rhombopora* (Fig. 1-8, 11-16), *Syringoclemis* (Fig. 9), *Leioclema* (Fig. 10)

ABSTRACT

A detailed study of the rhabdomesid cryptostome bryozoans from the Lower Permian Wreford Megacyclothem (Wolfcampian) of Nebraska, Kansas and Oklahoma was undertaken, attempting at all times to satisfy the two criteria of (a) reproducibility by other paleobryozoologists working on other ramose cryptostomes and (b) as wide-ranging applicability as possible to all bryozoan groups. To establish uniformly applicable concepts, techniques were standardized at all levels of the investigation. Collection (sampling) methods and labelling systems were based on established practices. Modification and extension of the cellulose acetate peel method facilitated examination of about 1,100 specimens. Statistics were computed (by an IBM 360/67) for a set of numerical morphological characters which had been standardly symbolized, in part based on previous work, in part new. These characters of the Wreford Rhabdomesidae were then coded into two-state form, and a cluster analysis with resultant dendogram was machine-generated.

Stratigraphic analysis indicated that very rapid facies changes occur at the Nebraska-Kansas and Kansas-Oklahoma borders with marine Wreford units giving way rapidly to continental redbeds and channel deposits.

The monothetic generic concepts *Rhabdomeson, Saffordotaxis,* and *Nicklesopora* are synonymized with *Rhombopora.* The generic concept *Syringoclemis* is expanded to include solid-ramose as well as epithecate-ramose zoaria, and the new species *Syringoclemis wrefordensis* is proposed. The skeletal morphology of the two Wreford rhabdomesids, *Rhombopora lepidodendroides* and *S. wrefordensis,* is examined in detail. The apparently non-analogous nature of the mesopores and acanthopores between the Trepostomata and Cryptostomata is explored. Comparison with the skeletal wall structure of the Fenestellidae indicates that laminations of the peripheral zone of the Wreford Rhabdomesidae may represent diurnal periodicity; based on this, the largest of the Wreford rhabdomesids were 18 months to two years old at death. Coordinated with this detailed skeletal analysis, the first reconstruction of ramose cryptostome soft-parts is proffered.

Rhombopora lepidodendroides shows extreme morphologic conservatism, but considerable random variability. The numerical characters of its type specimens show that its average morphologic condition throughout its range (Virgil through Wolfcamp) was constant. Within the Wreford, no systematic variation, either in a geographic (clinal) sense or stratigraphic (microevolutionary) sense, was observed.

Paleoecologically the Wreford Rhabdomesidae were most numerous in, and therefore apparently preferred, environments that were of normal marine salinity, quiet, and farthest from shore, that is, environments lithologically represented by calcareous shale in the Wreford. The competitive exclusion principle, on the basis of worldwide, North American, and Wreford evidence, may provide an explanation for *Rhombopora lepidodendroides'* dominance over, and eventual total replacement of, *Syringoclemis wrefordensis* in the Wreford Megacyclothem.

INTRODUCTION

PURPOSE OF STUDY

Bryozoans are a conspicuous element in the fossil record of the Paleozoic. Beginning in the Middle Ordovician and continuing to the late Middle Permian, one group, the so-called "stick bryozoans," makes up a large portion (often a majority) of the preserved fauna. This group, formally known as the family Rhabdomesidae of the order Cryptostomata, has not been extensively studied; in fact, even though they are so abundant, rhabdomesids are surprisingly often not reported in faunal lists of field paleontologists and geologists.

Deposits from the epeiric seas of the late Paleozoic of the midcontinental United States constitute a superb record of the greatest expansion and diversification, as well as the ultimate reduction and extinction, of the rhabdomesid cryptostomes. Cursory examination of samples from one of these deposits, the Wreford Megacyclothem (Lower Permian, Wolfcampian) of Kansas, indicated that it contains abundant and well-preserved

members of this family. Further, these fossils appeared to represent four, five, or possibly six different species distributed among perhaps three or four genera. Moreover, in the course of a preliminary attempt to identify the fossils, I soon found that there were no morphologic characteristics widely accepted for use in taxonomic work on this group of bryozoans. It was obvious, then, that here was a bryozoan group, extremely important numerically, zoologically, ecologically, stratigraphically and geographically, which had never been carefully examined.

The rocks from which the Wreford rhabdomesid specimens came have been intensively studied for 110 years, beginning with SWALLOW & HAWN (1858) and MEEK & HAYDEN (1860), and culminating with HATTIN (1957) and CUFFEY (1967). By adding to CUFFEY's original Wreford bryozoan collection, mainly by extending the study northward into Nebraska and southward into Oklahoma, I amassed a collection of approximately 100,000 rhabdomesid specimens. Each specimen could be located with precision lithologically, stratigraphically, and geographically. Consequently, many environmental parameters external to the bryozoans (such as nature of substrate, depth of water, turbidity of water, and distance from shore) had been previously interpreted or could be interpreted by me.

Because the taxonomy of the cryptostome bryozoans was apparently without widely utilized standards and apparently was based on monothetic ideas below the family level, careful study of the Wreford rhabdomesids potentially can make an extremely important contribution to bryozoan systematics. LAGAAIJ (1963) for the cheilostome bryozoan *Cupuladria canariensis,* and CUFFEY (1966, 1967) for the trepostome bryozoan *Tabulipora carbonaria,* had made extensive studies of single bryozoan species, studies which have led the way toward an in-depth understanding of intraspecific morphologic variability in bryozoans, as well as in colonial animals in general. More investigations like these are needed urgently in order to help formulate soundly based overall classifications of the various bryozoan groups, such as that developed by CHEETHAM (1968) for the metrarabdotid cheilostomes. This paper, therefore, is the first comparable study of morphological variability among cryptostome bryozoans of which I am aware. It also is, so far as I know, only the second such study on Paleozoic bryozoans of any group, and only the fourth such study ever undertaken on any bryozoans.

In the course of this investigation, I have developed and assessed much data on the microevolution, morphology, morphologic variability, ontogeny, ecology, and evolution of the Wreford rhabdomesids. Approximately 1,100 rhabdomesid colonies, collected from the Wreford Megacyclothem in Nebraska, Kansas, and Oklahoma, were sectioned, yielding a total of about 3,500 thin sections. The total number of measurements and counts made on these specimens and in this study is approximately 100,000-150,000, and consequently several computerized techniques were required to deal with this information.

In this paper, I will first review the historical background of the regional stratigraphy of the Permian in the central United States, and discuss the stratigraphy and facies of the Wreford Megacyclothem throughout its entire vertical and horizontal extent. I will also discuss the depositional environments as inferred from an analysis of the lithology and paleontology of each separate unit of the megacyclothem. Having examined this framework, I will describe each aspect of the rhabdomesids individually and in some detail. In addition, I will offer my conclusions concerning the taxonomy of the Permian rhabdomesid cryptostomes in general. Furthermore, I will make some speculations on overall rhabdomesid and bryozoan evolution and phylogeny. Finally, I will suggest a scheme for the classification and revision of Kansas Permian cryptostome taxa based on modern taxonomic concepts.

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The funding of this study was supplied by Geological Society of America Grant No. 1197-68. This money enabled me to do the field work and paid a great deal of the processing costs. Most of the additional expense was covered by National Defense Education Act funds.

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Finally, to my wife, SUZANNE, gratitude for her patience, her understanding, and for always believing this paper would exist.

STRATIGRAPHIC AND PALEONTOLOGIC BACKGROUND FOR WREFORD INVESTIGATIONS

HISTORICAL SUMMARY

Because of several excellent previous discussions (HATTIN, 1957; CUFFEY, 1966, 1967), only brief summaries of the important Wreford lithologies are given here. Further, CUFFEY (1966, 1967), ELIAS (1937), HATTIN (1957), LANE (1958, 1964), MCCRONE (1963), and MERRIAM (1962) have intensively studied these lithotypes in the Wreford and in formations of similar cyclic nature and age and have suggested the paleoenvironmental conditions under which each rock type was formed. In the course of the present study, I made some new observations regarding Wreford lithologies and stratigraphy; these are presented here, immediately following a brief summary of the major Wreford lithologies.

All of this information is further condensed and summarized in the generalized cross section of the Wreford Megacyclothem (Fig. 1) constructed by CUFFEY (personal communication, 1970). Figure 2 shows the area of outcrop of the Wreford rocks in Nebraska, Kansas, and Oklahoma, while Table 1 indicates the positions of the stratigraphic units involved in this study in those three states.

NEW OBSERVATIONS ON IMPORTANT WREFORD LITHOLOGIES

HATTIN (1957), supplemented by CUFFEY (1967), thoroughly discussed the characteristics and inferred paleoenvironments of the various rock types or lithologies found in the Wreford Megacyclothem in Kansas.

In order to set the background against which the environmental preferences of the Wreford rhabdomesid bryozoans must be understood, I will briefly summarize each of the major lithologies found in the Wreford Megacyclothem, simultaneously interweaving new observations and further discussion of each in appropriate places. Note that the lithologies are discussed more or less in transgressive order, that is, from continental to marine, as they would be encountered while going stratigraphically upward in a transgressive hemicycle.

Two lithotypes are quite probably continental deposits. These are the channel sandstones and channel conglomerates. Channel deposits are well known from the base of cyclothemic units (SIEVER, 1951; POTTER & SIEVER, 1956); they are generally interpreted as supralittoral to marginal marine deposits of river channels or their distributaries.

Channel sandstones (rare in the Kansas Wreford) are quite common at both the extreme northern and southern limits of the Wreford outcrop belt. Their appearance in these two regions coincides with thickening of the red shale units in the megacyclothem. These two phenomena indicate that the ancient shorelines of the Wreford sea are rapidly approached as one goes either northward into Nebraska from Kansas or southward into Oklahoma. These channel sandstones generally are red, thick to shaly bedded, fine grained, and quartzose. Locally, as at CY37, they contain poorly preserved impressions of fern fronds. In Oklahoma, these red channel sandstones make up a significant proportion of the redbed sequence. This complex of red shales and red channel sandstones, laterally equivalent to the marine carbonates and shales of the Kansas Wreford, may be interpreted as representing a low-lying coastal plain crossed by numerous stream courses.

ELIAS (1937) defined Phase 1 of the idealized lower Permian cycle as being red shales. Physically, the red shales lack graded beds, ripples or other such primary structures. This strongly suggests that the red shales represent subaerial coastal plain deposits. According to SCHMALZ (1968), discussing redbed origins in general, there would have been sufficient water in a warm, wet climate to dissolve iron-bearing minerals, thus releasing iron through chemical weathering. These iron-rich weathering products would then have been transported onto the broad coastal plains. Next, a long dry period required to dehydrate these primary weathering products would have ensued. Hematite, the product thereby formed from either ferric oxy-hydroxide or goethite (SCHMALZ, 1968, p. 277), would be extremely stable (SCHMALZ, 1958). Apparently, therefore, the Kansas region, during deposition of the Wreford red shales, was paleoclimatologically an environment of very high rainfall, all of which fell in six to eight months within each year. At the southern borders of Oklahoma, the long swing of the Wichita-Arbuckle highlands of Llanoria shed iron-rich primary weathering products northward all through the rainy season onto the flat coastal plains bordering the Wreford sea. There, in the long desert dry season, these iron-rich, fine-grained sediments were dehydrated into hematite. Few fossils are known from the red shales and muds (one locality only). The bryozoans found therein had had their projecting elements (spines, acanthopores) worn away. Other unmistakable signs of abrasion are evident in the associated fossil debris. Consequently, these fossils were either transported in and reworked into the red sediments upon subsequent transgression, or else were brought into the redbed-depositing area by erosion of older sediments. As the southernmost marine limit of the Wreford is approached (see Fig. 1), these shales and muds become increasingly silty and sandy. In Pawnee County, Oklahoma, some of the Wreford redbeds are sandy-matrix conglomerates, whose clasts display a "desert varnish" of iron (or manganese) oxide.

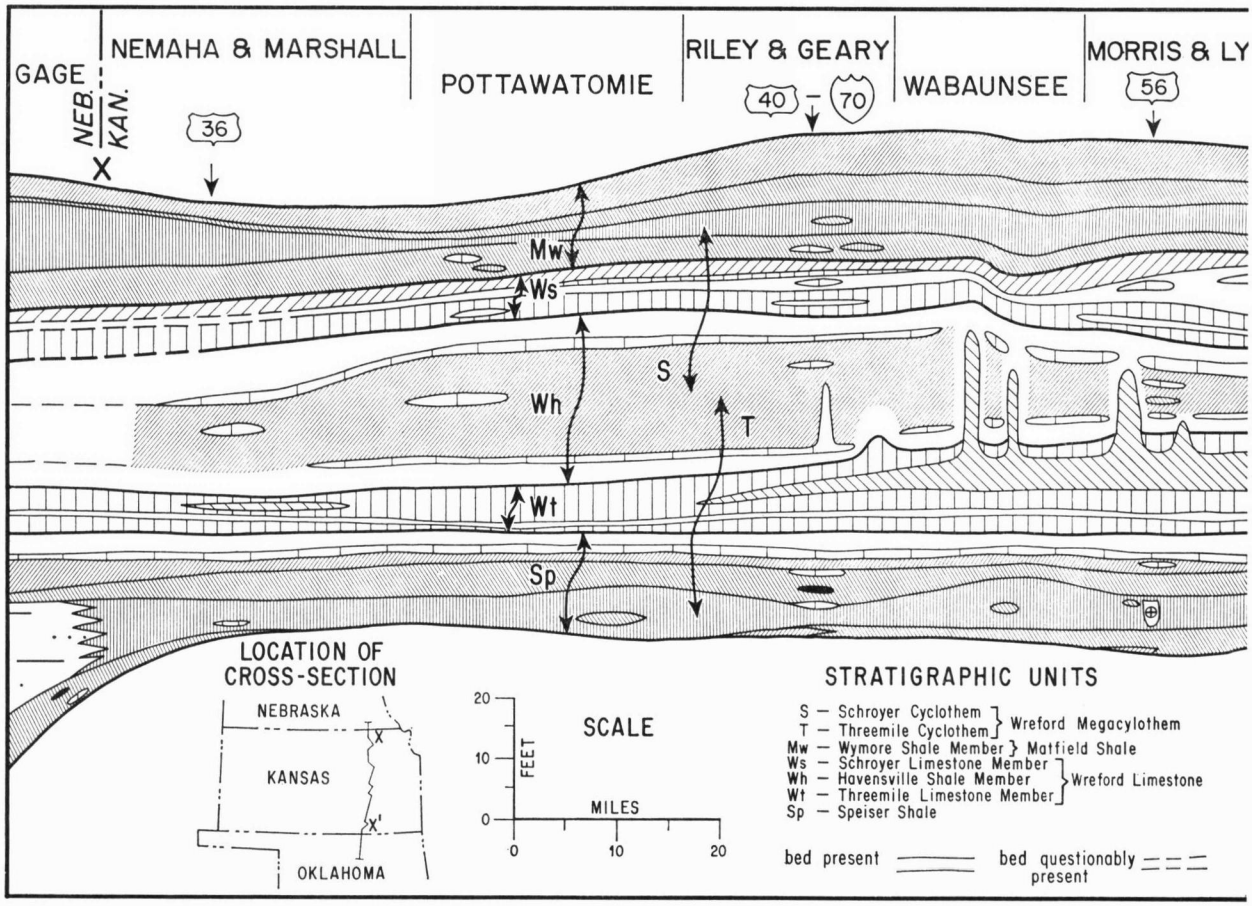
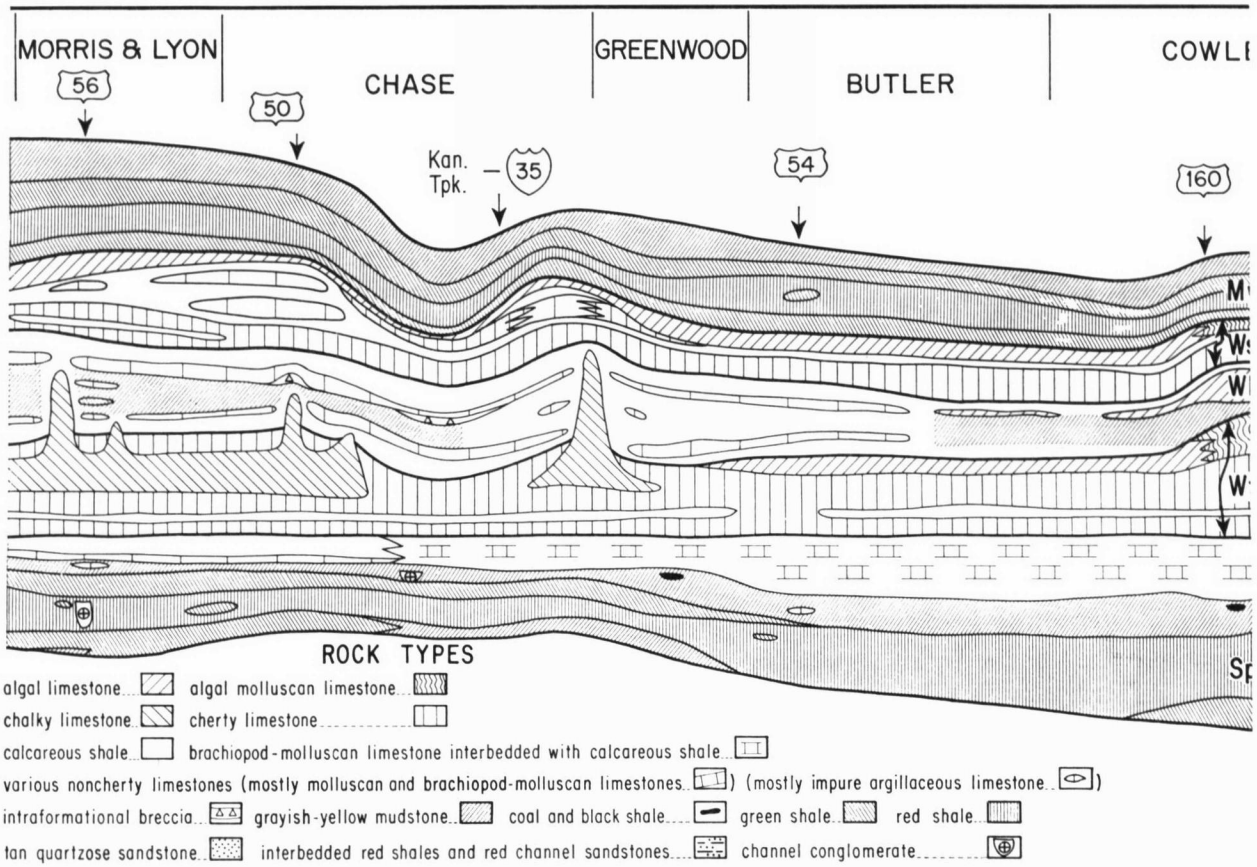


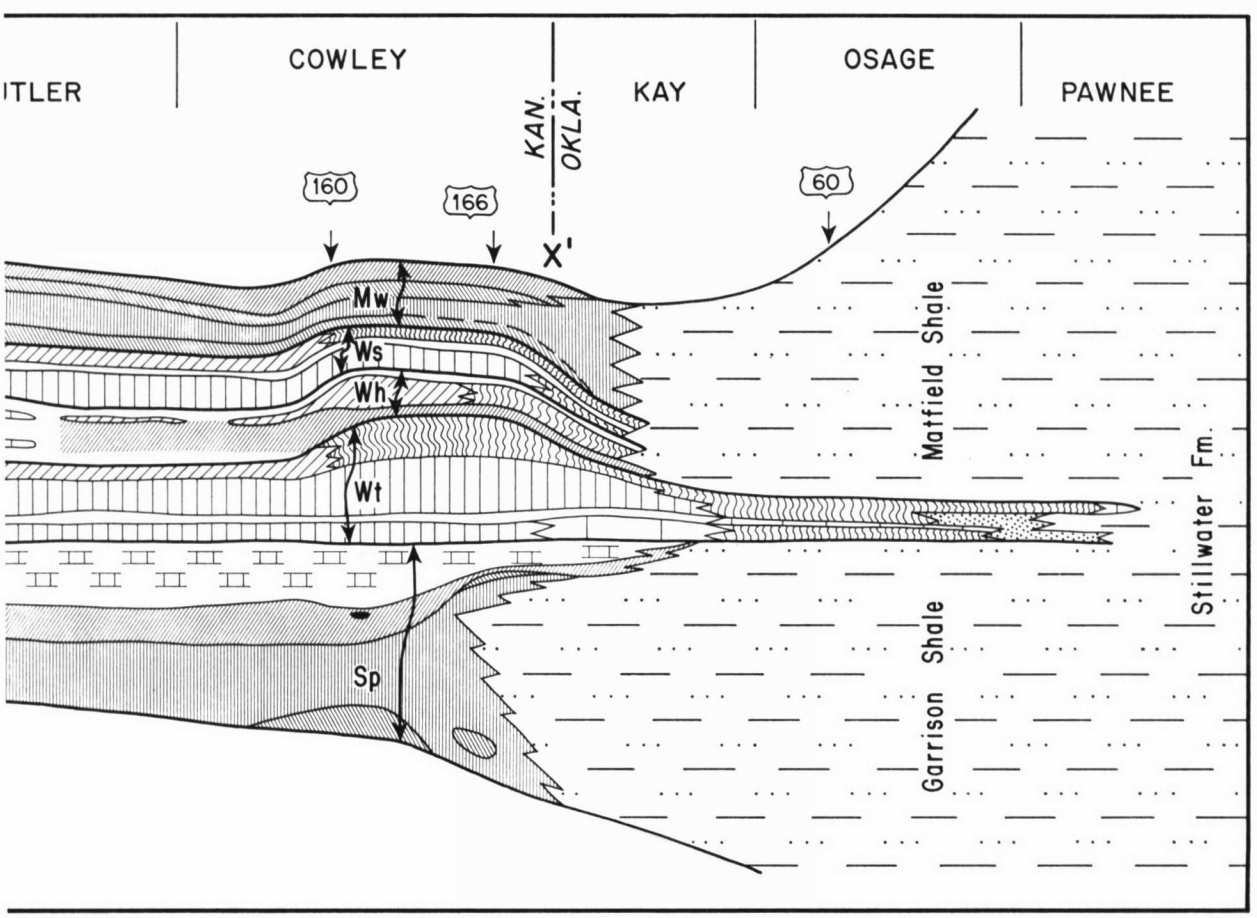
FIG. 1. Generalized north-south section of Wreford Megacyclothem rocks showing units differentiated by lithology and fossil content (northern part; central and southern parts shown on opposite page).

The green shales, Phase 2, represent what KRUMBEIN (1947, p. 105) referred to as "platform type." According to KRUMBEIN they represent stable platforms in shallow seas, which did not adjoin strongly positive areas. Fossils are rare. When fossils are present, they are interpreted (HATTIN, 1957, p. 53, 54, 85) as shallow-water, brackish populations. Ostracodes and occasional pinnules of *Neuropteris* comprise the bulk of the record. My interpretation (also that of MCCRONE, 1963, p. 64, 65) that these represent environments with water depths of less than two or three feet (low, intertidal mudflats or lagoons) is based on these facts: The red shales and mudstones are clearly continental, subaerial deposits; while the gray-yellow mudstones (see below), which overlie the green beds, clearly are slightly brackish marine deposits. Finally, the ELIAS (1937, p. 427) and HATTIN (1957, p. 85) interpretation that these are deposits representing deeper waters (up to 30 feet) would require that there was an entirely brackish Wreford sea of tremendous and unusually wide geographic extent.

Phase 3, the grayish-yellow mudstones, is almost always fossiliferous. Productid brachiopod spines, foraminifera, echinoderm plate fragments and spines, many ostracodes, bryozoans (very rare), and pelecypods (mostly *Aviculopecten*) are the most common faunal elements. HATTIN's interpretation (1957, p. 86)——that this represents waters slightly deeper and slightly more saline than Phase 2——is well supported and the reader is directed to his discussion for further information.

Phase 4, the molluscan limestone, is faunally characterized by the pelecypods *Aviculopecten, Mytilus,* and *Septimyalina.* NEWELL (1942, p. 19) states that mytilid clams prefer very shallow, very near-shore waters and show a tremendous temperature and salinity range toler-


MORRIS & LYON
CHASE
GREENWOOD
BUTLER
COWLE
56
50
Kan. Tpk.
35
54
160
M
Ws
W
W
Sp
ROCK TYPES
algal limestone
algal molluscan limestone
chalky limestone
cherty limestone
calcareous shale
brachiopod-molluscan limestone interbedded with calcareous shale
various noncherty limestones (mostly molluscan and brachiopod-molluscan limestones) (mostly impure argillaceous limestone)
intraformational breccia
grayish-yellow mudstone
coal and black shale
green shale
red shale
tan quartzose sandstone
interbedded red shales and red channel sandstones
channel conglomerate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Stillwater Fm.
Garrison Shale

ance. Also, inarticulate brachiopods (*Lingula* and *Orbiculoidea*) are most common in this phase. MOORE (1929, p. 469) indicates that modern linguloid brachiopods prefer shallow, brackish waters. The paleoenvironment of molluscan limestone, then, is shallow, is less than normal marine in salinity, and is faunally characterized by shelled invertebrates of euryhaline and eurythermal physiologies.

Phase 4 is represented in regressive hemicycles by algal and molluscan-algal limestones. My examinations of thin sections of these rocks show they are typically argillaceous micrites with algal (*Osagia*?), brachiopod, and pelecypod allochems up to about 50%. The presence of oolites, intraclasts, and (up to 10%) microsparite fragments suggests a moderately high energy environment. CUFFEY (1966, 1967) offers the most complete discussions of the varying regressive and transgressive aspects of these rocks, and the reader is directed there.

Several stratigraphic units within the Wreford megacyclothem are represented in southern Kansas by algal-molluscan limestones (HATTIN, 1957, p. 73, 75, 97, 99; CUFFEY, 1967, p. 12). When traced southward into Oklahoma, these become increasingly more sandy because of the progressively larger amounts of silt and fine-sand grains. Insoluble residue analysis of a few of these shows that the quartz clasts are subangular (0.3 and 0.4 on the POWER's scale of angularity), and are frosted. Eventually these rocks become so sandy that they may be classified as sandstones rather than limestone. As a consequence, the southernmost Wreford contains beds of light brown or tan, quartzose, spar-cemented sandstones.

Because these sandstones are significantly different from the channel sandstones previously observed in the Wreford of Kansas, I propose that these Oklahoma sandstones be recognized as a distinct rock type, herein termed a "tan quartzose sandstone," within the Wreford Megacyclothem. Massive to thin-bedded, weathering dark brown, this rock type when fresh ranges from white to dark brown in color. Its well-sorted, fine to medium-sized sand grains are all subangular (0.3 to 0.4) quartz. Many of the exposures of this sandstone show it to be penetrated by burrows or borings like those made by clams in the algal-molluscan beds farther north. Many exposures of this sandstone contain fossil pelecypods. Also, freshly broken surfaces frequently display dark brown blotches, which GREIG (1959, p. 106, 109) suggests are limonitized *Osagia* algae. Nodules and lenses of typically molluscan or algal-molluscan limestone occur in several places within the sandstone.

Both the regional stratigraphic relationships and the nature of the contained fauna clearly imply that the tan quartzose sandstone represents a very shallow, probably near-shore, brackish water environment. Because of the nature of the prevailing climate in northern Oklahoma today, considerable leaching has taken place, and it is probable that the calcareous material comprising the original rock is largely removed, secondarily intensifying the amount of quartz clasts present.

Returning to consideration of the Wreford algal-molluscan limestones in Oklahoma, I noted that in some places these rocks grade rather quickly into redbeds. In such cases, the intermediate or transitional phase is a red, nodular, calcareous, crinoid-pelecypod-brachiopod conglomerate with a red-shale matrix (for example, as at locality PW02). This transitional phase can probably best be considered as a molluscan-type argillaceous limestone.

Phase 5 in ELIAS' (1937) idealized Lower Permian cyclothems is represented in the Wreford by calcareous shale. Faunally, the calcareous shales are the richest Wreford phase. A flourishing, multi-phyla, multifaceted community existed, predominated (in the residue fossils) by filter feeding invertebrates (bryozoa and brachiopods). MCCRONE (1963) in the Red Eagle Cyclothem and IMBRIE, LAPORTE & MERRIAM (1959) in the Beattie Cyclothem interpreted this phase to have been deposited in 10 to 50 feet of water. CUFFEY (1966, 1967) concurred. Unless the sea was remarkably placid (admittedly a possibility), the lower figure (10 feet) is too low. On the other hand, unless the sea was extremely nonturbid, the higher bracket is too great. At the lower figure the turbulence at the bottom induced by wave action would probably destroy the delicate filter-feeding animals such as the slender branching bryozoans (the Rhabdomesidae, for example), the fenestrate bryozoans, and the pedically attached brachiopods. At the deeper value (50 feet), sufficient water clarity to enable algal growth would also mean (a) insufficient suspended organic debris and plankters to feed suspension-feeding organisms and (b) currents too low to move food past these same organisms. For these two reasons I prefer a narrower range of 10 to 30 feet. Further supporting discussion is offered later in this paper when discussing the paleoecology of the Wreford rhabdomesids.

The cherty limestones of the Wreford Megacyclothem represent Phases 6 and 7 (HATTIN, 1957, p. 63-68; CUFFEY, 1966, p. 22-23; CUFFEY, 1967, p. 12) of ELIAS (1937). Little can be added to the discussion of HATTIN and CUFFEY. It is perhaps worthwhile noting here that, through study of thin sections and exposed surfaces, I found the faunal constitution of the cherts and the limestone in which they are contained to be identical. One exception to this was noted in southern Nebraska. The cherts of the Threemile limestone at GA03 were fusulinid-bearing. The limestone itself was not observed to contain fusulinids.

NEW OBSERVATIONS ON STRATIGRAPHY OF THE WREFORD IN KANSAS

Previous workers (HATTIN, 1957; CUFFEY, 1966, 1967) have adequately described the stratigraphic relationships of the Wreford Megacyclothem's components in

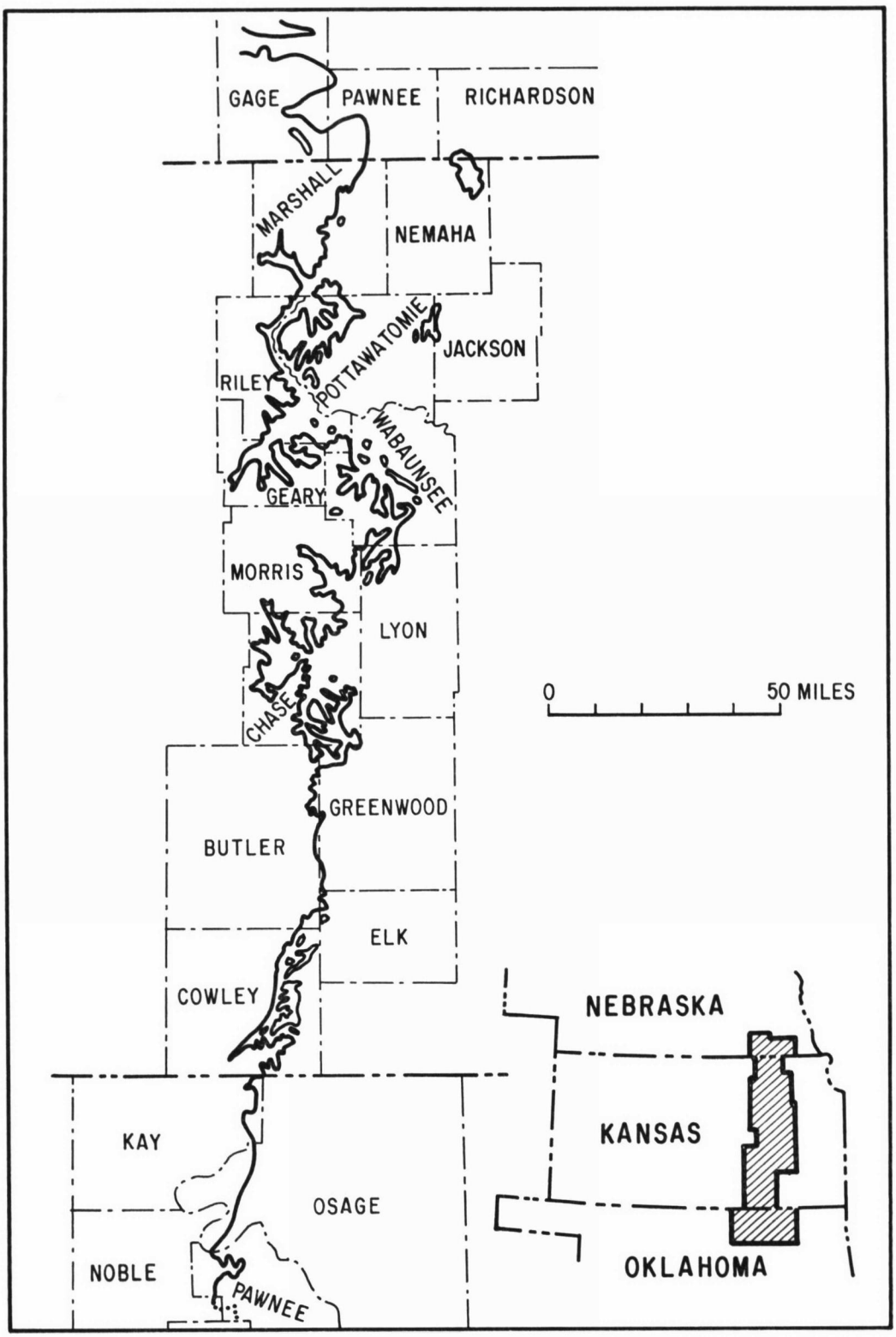
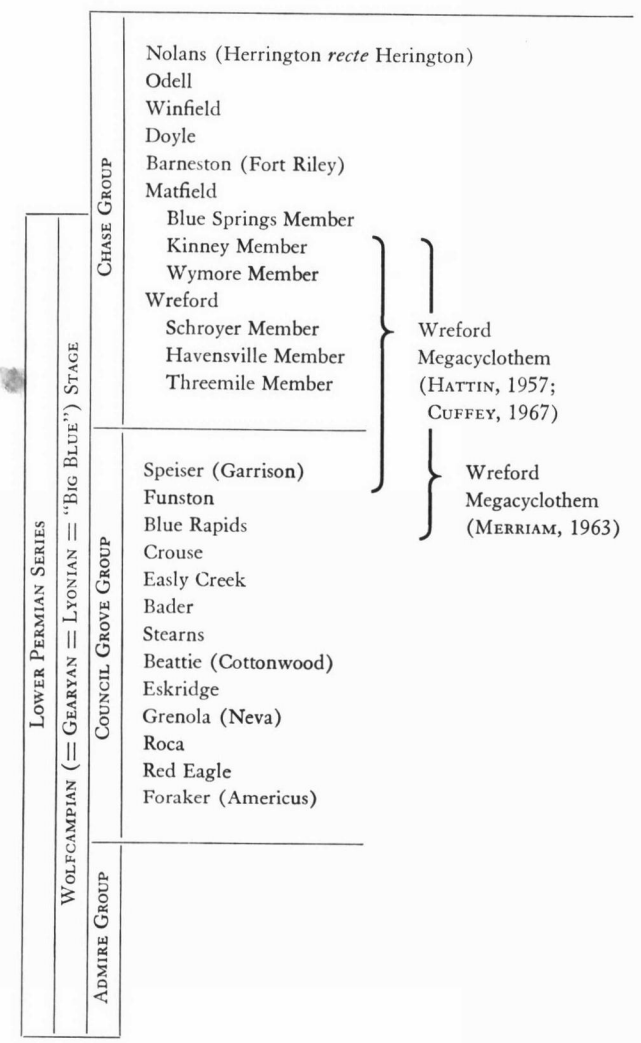


FIG. 2. Outcrop of Wreford Limestone (Lower Permian) in Nebraska, Kansas, and Oklahoma (adapted from Geologic Bedrock Map of Southeastern Nebraska, 1966; Geologic Map of Kansas, 1964; and Geologic Map of Oklahoma, 1964).

TABLE 1. *Stratigraphic Units in the Lower Permian of Kansas and Nebraska; Oklahoma Nomenclature (after Branson, 1960) Appears in Parentheses.*



Kansas. Several observations made during my study of Wreford rhabdomesids also increase our understanding of this topic.

As previously noted (CUFFEY, 1967, p. 13-14), the exact stratigraphic relationships of the lower and middle Havensville rocks to the upper Threemile rocks is difficult to assess. Consequently, I carefully examined the contacts of these units in several areas to clarify this relationship. In no exposure did interfingering occur. As CUFFEY (1967, p. 13) observed, the continuously transitional nature of contacts between successive rock types from the upper Threemile cherty limestone to the middle Havensville gray-yellow mudstone in northern Kansas implies that these rocks represent essentially continuous sedimentation. In southern Kansas, similar transitional contacts can be seen between the gray-yellow mudstone of the middle Havensville and the underlying algal or algal-molluscan limestones in the uppermost Threemile. Therefore, continuous sedimentation is implied for southern Kansas from late Threemile into early Havensville time. Consequently, the algal and algal-molluscan limestones of the uppermost Threemile appear to be time equivalent to at least the calcareous shale and molluscan limestone of the lower Havensville in northern Kansas. This inference agrees with that drawn previously (CUFFEY, 1967, p. 14).

On the other hand, where middle Havensville rocks directly overlie the thick upper Threemile chalky-limestone buildups in central Kansas, the contacts are sharply defined, suggesting a pause in sedimentation there. This observation tends to confirm HATTIN's (1957, p. 94) conclusion that the chalky limestone buildups represent only late Threemile time rather than being laterally equivalent to the lower Havensville depositional interval.

Variations in the thickness of the chalky limestones within the upper Threemile in central Kansas have suggested that significant relief existed on the floor of the Wreford sea at the time these rocks formed (HATTIN, 1957, p. 68-70; CUFFEY, 1967, p. 12-14). HATTIN (1957, p. 69) noted coarse clastic limestones adjacent to the chalky-limestone buildups, and interpreted them as confirming that idea.

In addition to these observations, intraformational breccias locally are observed to overlie the chalky buildups (locality CH05, as an example). Since the shallower bottoms over the chalky mud banks would presumably be more often disturbed, it is not unreasonable to expect such deposits in these places. These breccias, therefore, tend to lend credence to earlier interpretations of the paleoenvironment represented by the chalky limestones.

Whenever I encountered plant-bearing, coaly, or carbonaceous fine-grained sediments, in the Wreford, I took samples for palynological examination. These samples were processed by standard pollen maceration techniques, as outlined by GRAY (1964), and were examined for palynomorphs. The detailed results of this work will be published subsequently as a separate study.

Of immediate relevance, however, are the preliminary observations from one locality, BU04, as they bear upon the Wreford regional stratigraphic picture. There, the calcareous shale at the base of the Havensville is carbonaceous, and yielded palynomorphs. Also, plant fragments resembling *Walchia,* an early coniferophyte, and *Callipteris,* a pteridosperm, are preserved here as ephemeral, noncollectable films of vitrinitic material. Palynomorphs which I recovered from this horizon and locality include monosaccate and bisaccate pollen grains of the genera *Florinites, Lueckisporites, Alisporites, Pityosporites,* and *Protohaploxypinus*; thick-walled, large, trilete (fern) spores also occur there. The saccate palynomorphs are well preserved. Their sacci, though pitted through post-depositional oxidation, are attached to the central bodies

in nearly all of the specimens. The trilete spores are also very nicely preserved.

This deposit apparently represents a local accumulation of vascular plant material, washed out into the Wreford sea from a nearby vegetated coast, perhaps located a short distance east of the present Wreford outcrop belt. The vesiculate palynomorphs are quite delicate, and thus presumably might not endure long transport; however, TRAVERSE (1967) found comparable modern pollen far out on the Bahama Banks, which suggests the contrary.

As noted by CUFFEY (1967, p. 10), the carbonate mound buildups of the upper Threemile chalky limestone facies occur just north of the site of the so-called "Greenwood Shoal." This shoal was active in Americus (basal Council Grove) time (HARBAUGH and DEMIRMEN, 1964) and during Beattie (middle Council Grove) time (IMBRIE, LAPORTE and MERRIAM, 1959; LAPORTE, 1962). South of this shoal area, the uppermost Threemile assumes its algal or algal-molluscan limestone facies (see CUFFEY, 1966, 1967). The position of the spore- and pollen-bearing site, BU04, is just southwest of the earlier Greenwood shoal position. Just north of the shoal areas, at locality LY02, the middle Speiser contains a stream channel deposit with amphibian and reptile bones mixed in with quartz, rock fragment, and chert clasts of two to six millimeter size.

This evidence collectively seems to imply, by four lines of reasoning, that the Greenwood Shoal of Americus and Beattie time existed during Wreford time as well. First, the lower Havensville calcareous shale south of the shoal's previous position contains local accumulation of vascular plant debris apparently derived from nearby land areas; the proximity of the land areas could be due to the eastern part of the shoal being subaerially exposed. Second, just north of the shoal's previous position, the middle Speiser contains a channel conglomerate composed of land-derived sediments, again presumably from nearby land areas. Third, the chalky limestone carbonate mounds were built, entirely north of the shoal's position. Fourth, the uppermost Threemile in the latitude of the shoal changes from the normal cherty limestone (deep water) to algal limestone (shallow water), entirely south of the presumed shoal area. However, I found no good exposures of the Wreford carbonates on the Greenwood Shoal, and also saw no indisputable evidence of turbulent shoal water in the Wreford rocks in this region. Further carbonate-petrographic work is obviously needed to finally resolve this question. Reference to Figure 1 will aid the reader in more clearly visualizing the space-time relationships of these rocks.

STRATIGRAPHY OF THE WREFORD IN NEBRASKA

Although largely obscured by Pleistocene drift, the Wreford Megacyclothem extends northward into Nebraska a distance of about thirty miles. There, it disappears beneath the Cretaceous (Dakota) overlap. All the Wreford localities seen by me, however, are near the southern border of the state.

Within the first three miles north of the Kansas-Nebraska boundary, the middle Speiser is noticeably changed. First, it is considerably thicker. Second, it consists of interbedded red shales and fine-grained channel sandstones, rather than being entirely red shale. Also, the underlying lower Speiser contains occasional lenses of dark gray to dark brown shale, possibly comparable to the black shales seen farther south (CUFFEY, 1967, p. 11). These rocks suggest that the northern shore of the Wreford sea, at least in mid-Speiser time, lay at, or only a short distance north of, the Kansas-Nebraska line.

The upper Speiser and the entire Threemile in southernmost Nebraska are essentially the same as they are in northernmost Kansas. The only obvious difference is that the chert in the lower Threemile locally (GA03) contains small fusulinids *(Triticites)*. Consequently, I suggest that the shoreline had retreated somewhat farther northward as upper Speiser time began.

I was unable to find any exposures in Nebraska of the Havensville and Schroyer (see my comment in the "Wreford Megacyclothem Locality Register" appended to GA02). Presumably these units would be much the same in Nebraska as they are in northern Kansas.

The lower Wymore continues northward into Nebraska from Kansas as a thick green shale or mudstone. The middle Wymore, still a red shale as in Kansas, continues but thickens. I interpret this to indicate that the shoreline had advanced southward during middle Wymore time and was quite near at hand at the close of the middle Wymore.

STRATIGRAPHY OF THE WREFORD IN OKLAHOMA

Most of the Wreford units recognized in southern Kansas persist into Oklahoma for only a few miles, grading then into thick redbeds. Parts of the Threemile, however, extend much farther south, into Pawnee County, about 45 miles south of the state line. The other marine limestones in the Permian of Kansas disappear southward into Oklahoma. In particular, the Funston Limestone below the Speiser, and the Kinney Limestone above the Wymore, are both gone within the northernmost ten miles of Oklahoma. As a result, south of the point of their disappearance, on down to the point where the last Wreford beds are gone, somewhat different stratigraphic nomenclature is applied to these rocks. The Threemile Limestone Member is simply referred to as the Wreford Limestone, the largely redbed sequence below it as the Garrison Shale, and the largely redbed sequence below it as the Matfield Shale. South of the point of disappearance of the Wreford, the redbeds above and below merge into

indistinguishability, and are, therefore, collectively labelled the Stillwater Formation (GREIG, 1959, p. 75, 107; DOTT, 1941, p. 1679; BRANSON, 1960, p. 331-335).

As the Wreford Megacyclothem passes into northern Oklahoma from Kansas, other changes in its stratigraphy can be observed. Just north of the Kansas-Oklahoma line, the middle Speiser changes from a red shale to a complex of interbedded red shales and red channel sandstones, which rapidly thicken southward. The upper Speiser marine rocks (grayish-yellow mudstone, brachiopod-molluscan limestone, calcareous shale) thin and are replaced in the section by interbedded red shales and red channel sandstones within the first ten miles of northern Oklahoma.

The lower Threemile, highly cherty limestone over most of Kansas, loses its chert gradually in southernmost Kansas and grades into a non-cherty brachiopod-molluscan limestone at the state boundary. This in turn grades into algal-molluscan limestone with superbly preserved *Osagia*-type algae and vertical burrows or borings, about fifteen miles farther south. Becoming increasingly sandy southward, the algal-molluscan limestone passes into tan quartzose sandstone in northern Pawnee County, and then rapidly into red shales and red channel sandstones in central Pawnee County.

The calcareous shale forming the middle Threemile throughout Kansas persists as such about fifteen miles into Oklahoma. It then changes into a thin (generally three to six inches), shaly brachiopod-molluscan limestone, which dies out approximately 35 miles south of the Kansas-Oklahoma border.

The precise stratigraphic relationships of the upper Threemile and lower Havensville equivalents are more difficult to determine than are those described above. Future detailed stratigraphic and petrographic work on these rocks in this region will eventually be required to determine the time relationships within this sequence.

However, in the interim, I suggest the following, based on CUFFEY (personal communication, 1970), as being the most probable interpretation of these relationships.

In southernmost Kansas, the upper Threemile is a cherty limestone, and the lower Havensville is an algal-molluscan limestone. Within the ten miles into Oklahoma both thin to about one-third their thickness in Kansas and are replaced laterally by an algal-molluscan limestone. Because of the thickness changes and drastic lithofacies changes taking place above these rocks, I tentatively suspect that this thinner algal-molluscan limestone represents only the lower and middle portions of the upper Threemile of Kansas.

Some 25 miles south of the state line, the lower part of this algal-molluscan limestone (that part equivalent to the lower beds of the upper Threemile; CUFFEY, 1967, p. 74, fig. 22) becomes tan quartzose sandstone, and finally, redbeds about fifteen miles farther south. Simultaneously, 25 miles south of the border, the upper part of the algal-molluscan limestone (that part equivalent to the middle beds of the upper Threemile; CUFFEY, 1967, p. 74, fig. 23) continues on southward finally becoming a red, nodular, molluscan-type limestone (PW02, for example) about 45 miles south of the state line, before it disappears into the interbedded red shales and red channel sandstones of the Stillwater Formation.

On the other hand, the cherty limestones of the upper part of the upper Threemile may pass laterally into first algal-molluscan limestone and then quickly pass into redbeds. This all would happen within the northernmost fifteen miles of Oklahoma, as the upper Threemile carbonate section rapidly and drastically thins southward. Similarly, the algal-molluscan limestone thought to represent the lower Havensville may very quickly grade into redbeds only about five miles below the state line.

The stratigraphic relationships of the higher units of the Wreford Megacyclothem in Oklahoma are much clearer, happily, than those just discussed. Traced southward from the Kansas-Oklahoma boundary, these units at first thin slightly. Then, about five miles below the border, they very rapidly pass into a thick sequence of interbedded red shales and channel sandstones. I saw none of these higher Wreford units anywhere south of northernmost Kay County. This can be interpreted as indicating that the southern shoreline of the Wreford Sea was essentially at this position throughout middle and late Havensville, Schroyer, and early Wymore time. Such an interpretation lends support to the idea (CUFFEY, 1967, p. 10-13, 87) that environmental factors other than simple transgression-regression of the Wreford Sea caused the complex cyclothemic sedimentation observed in the Wreford Megacyclothem.

Calcareous shale represents the middle Havensville in northernmost Oklahoma, as it also does in parts of southern Kansas. Calcareous shale overlying algal-molluscan limestone comprises the Oklahoma, as well as the southernmost Kansas, upper Havensville. The cherty limestone of the lower Schroyer tends to lose its chert in southernmost Kansas, and grades into an algal-molluscan limestone at the state line. The middle Schroyer and upper Schroyer continue unchanged into Oklahoma as calcareous shale and algal-molluscan limestone, respectively. The lower Wymore is extensively covered everywhere looked for south of northern Cowley County, Kansas. Presumably it continues southward from there as a thin green shale.

Represented by red shale in southern Kansas and northern Oklahoma, the middle Wymore thickens and changes into interbedded red shales and red channel sandstones within the first five miles south of the state line. Further south these redbeds thicken rapidly, in part at the expense of the Wreford marine beds, in part due to an increased supply of detrital sediments.

WREFORD MEGACYCLOTHEM LOCALITY REGISTER

The listing which follows includes only localities not given by CUFFEY (1966, 1967). These are plotted in figures which accompany the text (Fig. 3-5). Most of the bryozoans used in this study were collected from localities in Kansas already adequately described by CUFFEY (1967, p. 89-94). To be consistent with the system introduced by him, I have used his format and nomenclature.

In the list, after the number and description for each locality, the stratigraphic units exposed therein are indicated in terms of their informal divisions. These are: upper *(u)*, middle *(m)*, and lower *(l)*; Speiser Shale (Garrison Shale) is abbreviated to *Sp*, Threemile Limestone Member (of Wreford Limestone) to *Wt*, Havensville Shale Member to *Wh*, Schroyer Limestone Member to *Ws*, and Wymore Shale Member (of Matfield Shale) to *Mw*. Following next is an indication of whether the exposure(s) is very good (VG), good (G), fair (F), poor (P), or very poor (VP). Then, for a few, published references to the particular locality are cited.

FIG. 3. Wreford localities in southern Nebraska (separately numbered in counties).

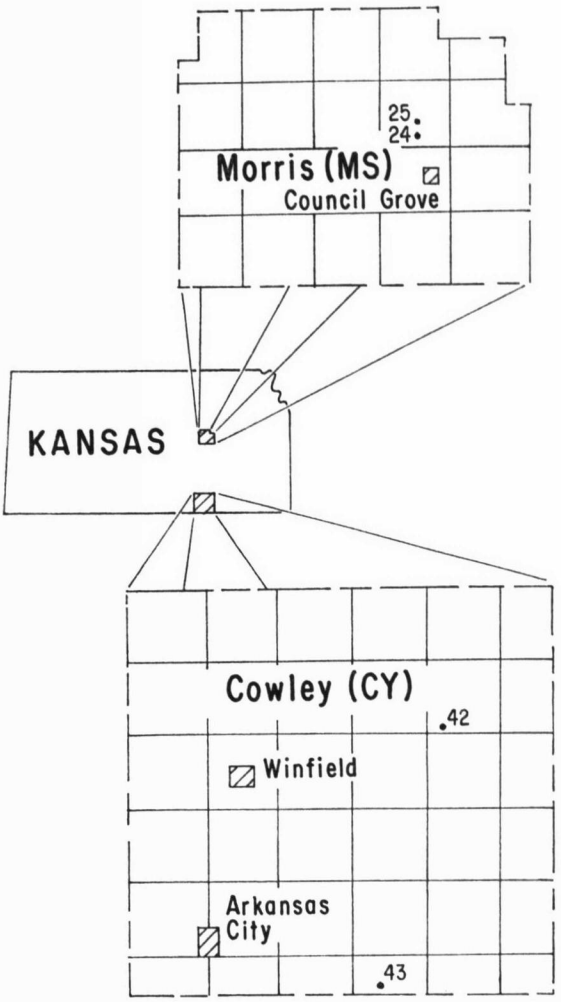


FIG. 4. Wreford localities, additional to those of CUFFEY (1966, 1967), in Kansas (separately numbered in counties).

COWLEY COUNTY, KANSAS (Figure 4)

CY42: Stream cut, 0.2 mile southwest of junction of U.S. Hwy. 160 and county road, 3 miles east of Burden; center of NE¼ NE¼ sec. 31, T.31S., R.7E. *m*Sp — *u*Wt; G.

CY43: Stream cut, 1.4 miles north of Oklahoma border on Cowley Co. Rd. 13 and 0.1 mile south of Shellrock Creek; NE¼ SE¼ sec. 8, T.35S., R.6E. *m*Sp — *l*Wt; VG.

GAGE COUNTY, NEBRASKA (Figure 3)

GA01: Ravine on hillside, 0.3 mile north of railroad crossing on road, 2½ miles east of Wymore; E edge of NE¼ sec. 27, T.2N., R.7E *l* — *u*Mw; VP. (CONDRA & UPP, 1931, p. 37).

GA02: Pasture exposure, 0.5 mile northwest of junction of county roads, 3½ miles southeast of Wymore; NW¼ SE¼ sec. 26, T.2N., R.7E. Not Ws; P. (CONDRA & UPP, 1931, p. 33, incorrectly identify this exposure as Schroyer. It is actually the cherty limestone of the Florence Flint Member of the Barneston Formation.)

GA03: Road cut on Nebraska Hwy. 8, 2.4 miles east of Barneston; center S edge SE¼ SW¼ sec. 16, T.1N., R.8E. *l*Sp — *l*Wt; VG.

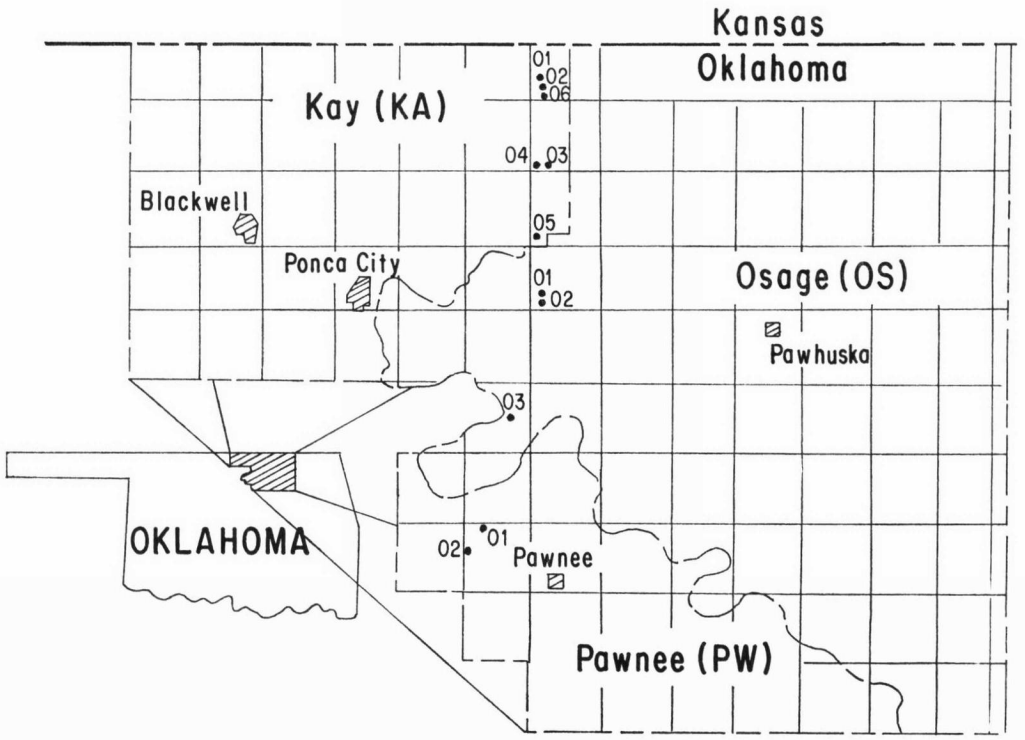


FIG. 5. Wreford localities in northern Oklahoma (separately numbered in counties).

GA04: Railroad cut, 0.3 mile northwest of railroad crossing on county road, 2 miles east of Wymore; W½ NE¼ sec. 27, T.2N., R.7E. *m* — *u*Mw; G.

KAY COUNTY, OKLAHOMA (Figure 5)

KA01: Road ditch on county road, 0.2 mile north of bridge over Myers Creek, ½ mile southeast of former site of Hardy; NE corner sec. 30, T.29N., R.5E. *m*Sp — *l*Ws; F. (HEALD, 1916, p. 22).

KA02: Road cut on country road, 0.1 mile south of bridge over Myers Creek, ¾ mile southeast of former site of Hardy; NE¼ SE¼ NE¼ sec. 30, T.29N., R.5E. *m*Sp — *u*Ws; VG.

KA03: Gullies in pasture, 0.3 mile east of center of junction of county roads, 6½ miles north of Kaw City; S edge of SW¼ SW¼ sec. 31, T.28N., R.5E. *m*Sp — *u*Wt, *m*Mw; F.

KA05: Butte top, 0.2 mile northwest of junction of county roads, 1¼ miles east-northeast of Kaw City; SW¼ SW¼ sec. 31, T.27N., R.5E. *m*Sp, *l* — *u*Wt; F.

KA06: Road cut on county road, 0.4 mile south of bridge over Myers Creek, 1 mile southeast of former site of Hardy; center W edge sec. 29, T.29N., R.5E. *m*Mw; P.

MORRIS COUNTY, KANSAS (Figure 4)

MS24: Road cut on Kansas Hwy. 57-177, 0.7 mile south of bridge over Munkers Creek; center NW¼ sec. 26, T.15S., R.8E. *m* — *u*Mw; F.

MS25: Road cut on Kansas Hwy. 57-177, 0.5 mile south of bridge over Munkers Creek; center N½ NW¼ sec. 26, T.15S., R.8E. *m* — *u*Ws; G.

OSAGE COUNTY, OKLAHOMA (Figure 5)

OS01: Road cut on new U.S. Hwy. 60, 4.7 miles west of railroad crossing at east edge of Burbank; center S edge SE¼ SE¼ sec. 30, T.26N., R.5E. *m*Sp, *l* — *u*Wt, *m*Mw; F.

OS02: Gully in pasture, 0.0 - 0.1 mile south of old U.S. Hwy. 60, 4.7 miles west of railroad crossing at east edge of Burbank; NE¼ NE¼ sec. 31, T.26N., R.5E. *m*Sp, *l* — *u*Wt; F.

OS03: Butte top, 0.3 mile west-southwest of junction of county roads, 10 miles west of Fairfax; SE¼ NW¼ sec. 21, T.24N., R.4E. *m*Sp, *l* — *u*Wt; P.

PAWNEE COUNTY, OKLAHOMA (Figure 5)

PW01: Road cut on Oklahoma Hwy. 15, 4.0 miles west of junction with Oklahoma Hwy. 18, 6 miles south of Pawnee; SW corner sec. 3, T.22N., R.4E. *m*Sp, *l* — *u*Wt; G. (GREIG, 1959, p. 196, 108, 168).

PW02: Road cut on county road, 1.5 miles south of junction with Oklahoma Hwy. 15 (junction 7.0 miles west of junction with Oklahoma Hwy. 18), 7½ miles northwest of Pawnee; center W edge sec. 18, T.22N., R.4E. *m*Sp, *u*Wt, and *m*Mw; G. (GREIG, 1959, p. 109).

ZOARIAL GROWTH FORMS

CUFFEY (1967, p. 16-17) defined several gross forms which bryozoan colonies from the Wreford assume.

The encrusting threadlike zoarial growth form, ETL in plates, figures, tables, and discussions, are delicate,

anastomosing traceries upon echinoid, crinoid, pelecypod, bryozoan, and brachiopod surfaces and are commonly referred to species of ctenostome bryozoans such as the genera *Vinella* and *Condranema*. Some ETL are zoaria composed of thin, calcareous tubes, semicircular in section; these colonies are perhaps referable to cyclostome bryozoan genera in the Diastoporidae and Tubuliporidae.

Encrusting sheetlike zoaria, ESL, are laminar, thin (0.5 to 2 mm in thickness) encrustations of brachiopod and pelecypod shells, bryozoan, echinoid and crinoid surfaces, or are simply found unattached to any object. The latter occurrence is usually inferred to indicate original encrustation on surfaces which are not preserved as fossils, such as algal fronds and the stem and leaf surfaces of marine vascular plants. Thin sections indicate that the majority of the ESL are various genera of the fistuliporid cyclostomes. Cuffey (1966, 1967) suggests affinities with *Cyclotrypa, Eridopora,* and *Fistulipora*. Other ESL are, occasionally, the stenoporid trepostome *Tabulipora carbonaria,* and various rhabdomesid cryptostomes.

The ESL, because of their encrusting nature, possess zooecial openings upon one surface only. The third group, the bifoliate zoaria, BIF, have zooecial apertures opening on two opposed surfaces. These zoaria are frondose, thin (1.0 to 3 mm thick) bryozoans all belonging to the hexagonellid cyclostome genus *Meekopora*. From examination of excellent silicified material of equivalent age in the collections of the Smithsonian Institution (see also, Moore & Dudley, 1944, pl. 40, fig. 1), I interpret the fragments observed in the Wreford samples as portions of large, erect stands of intricately intertwined, bifurcating and inosculating zoaria up to 15 centimeters in height.

Delicate branching zoaria, DBR, are thin (a diameter range of 0.5 to 4 mm), cylindrical, commonly dichotomously branching, erect (zoarial height up to 25 millimeters) zoaria. These are predominately rhabdomesid cryptostome bryozoans and are the principal objects of this study. Previously, the DBR of the Wreford Megacyclothem had been scattered among several genera, in four families of the Cryptostomata (Rhabdomesidae, Arthrostylidae, Ptilodictyidae, and Rhinidictyidae) and occasionally also one family of the Trepostomata (Stenoporidae).

The robust pinnate zoaria, RPI, as their name implies, appear as stout feathers. Their axial portion is one to several millimeters in thickness. From this axis, at frequent intervals, arise stout side branches at steep angles. When the side branches branch again, the whole zoarium may be ten to 15 millimeters tall and some five to eight millimeters wide, looking much like a miniaturized set of stag antlers. This zoarial growth form appears to be made up entirely of the acanthocladiid cryptostome bryozoan *Acanthocladia*.

Robust branching zoaria, RBR, consist almost entirely of colonies of *Tabulipora carbonaria*. These are the largest and most conspicuous bryozoans in the Wreford Megacyclothem, being three to 15 millimeters in diameter and ranging to perhaps 80 millimeters in height, cylindrical, and commonly branched several times. These are the basis of Cuffey's (1966, 1967) work, and the reader is directed there to examine this trepostome in detail. Rarely, a fistuliporid cyclostome bryozoan will have this zoarial growth form. Also, rarely, a few rhabdomesid cryptostomes range up to three and four millimeters in diameter, thus placing them in the lower size range of the RBR.

The delicate pinnate zoarial growth form, DPI, apparently is made up entirely of the acanthocladiid cryptostome bryozoan *Penniretepora*. These are characterized by a slender (about 0.25 mm in diameter) central stem, from which opposed, very slender (less than 0.125 mm) branches are planarly disposed. No secondary branching (as in the RPI) occurs. Occasionally, on a bedding plane, complete colonies are preserved. These may be as long (high) as 15 millimeters. More commonly, only fragments are found, these being two to five millimeters in length.

The eighth zoarial growth form, the fenestrate zoaria, abbreviated FEN, are flat or slightly curved, thin, lacey or trellised sheets, commonly as large as 25 by 25 millimeters in extent. The fenestellid cryptostome bryozoan genera *Fenestella* and *Polypora* are certainly present. *Thamniscus,* in the same family, is probably also represented in the Wreford Megacyclothem. Possibly, the acanthocladiid cryptostomes *Septopora* and *Synocladia* are present as well.

METHODS OF STUDY

COLLECTION METHODS

Rocks other than resistant lithotypes are not well exposed in northern Kansas and southern Nebraska. Limestones, being resistant, are expressed topographically as hill crests, with the overlying shales and mudstones being eroded away, or else as benches in midslope, with the overlying and underlying shales being grassed- and slumped-over. In southern Kansas and northern Oklahoma, because of a drier climate, shales and mudstones, where present, are more often naturally exposed, as in dry stream gullies. Consequently, road cuts are primary sources of samples in the northern portion of the Wreford Megacyclothem outcrop belt, while road cuts and natural outcroppings both contribute in the southern portion.

Samples were collected from the limestone units by examination of large surface areas and vertically exposed surfaces in outcrop; that is, penetration of the samples

into the mass of the limestone units was shallow. In addition to collecting bryozoans (and other fossil material) from the exposed vertical and horizontal surfaces, large, oriented samples of each lithology were taken as well. These samples were later crushed and examined for bryozoa. A chip of each such sample was either thin-sectioned or reserved for such purpose.

Shales, mudstones, and siltstones were sampled by excavating deep into the exposure, usually until some appearance of "freshness" was evidenced. Then approximately one liter was taken as a bulk sample. "Freshness" in these sediments is shown by wetness, lack of modern plant roots and insect larvae, and blocky texture in the mudstones or indications of bedding in the shales, or cohesiveness in the siltstones. Having exposed a vertical, clean, uncontaminated face, the bulk samples were taken in thirds (designated lower, middle, upper) when the unit was greater than one and one-half feet thick and in halves (upper and lower) when the unit was one and one-half feet thick or less.

SAMPLING METHODS

CUFFEY (1966, 1967) discussed collection methods. He briefly pointed out the value of securing fresh, uncontaminated bulk samples rather than simply picking up material that had weathered free on the outcrop surfaces. In Table 2, I have presented numbers which I generated by collecting from the same outcrop and horizon as CUFFEY had (CUFFEY, 1966, table 3, p. 63; CUFFEY, 1967, table 3, p. 17). His conclusion that one tends to see larger species more rapidly, thus they are overrepresented in most collections, is true.

TABLE 2. *Comparison Between Two Observers, Collecting Bryozoans from Material Weathered Free at the Same Locality and Horizons, and the Same Two Observers Picking Bryozoans from a Post-kerosene-treatment, Uncontaminated Fresh Shale Sample From the Same Horizon and Locality.*

Locality MS06: Upper Havensville Calcareous Shale Horizon

ZOARIAL GROWTH FORM	BRYOZOANS PICKED FROM MATERIAL WEATHERED OUT			BRYOZOANS PICKED FROM UNCONTAMINATED FRESH SHALE SAMPLE		
	Cufley	This Report	Combined	Cuffey	This Report	Combined
ETL	00%	TR	TR	00%	00%	00%
ESL	04%	03%	03%	TR	02%	01%
BIF	00%	00%	00%	00%	TR	TR
DBR	21%	67%	52%	09%	27%	22%
RPI	00%	02%	01%	16%	13%	14%
RBR	69%	11%	30%	TR	TR	TR
DPI	00%	00%	00%	10%	05%	05%
FEN	06%	15%	13%	64%	53%	57%
TOTAL BRYOZOANS	67	136	203	220	511	731

A second point, not then obvious, is made by my data; the eye of the collector is somewhat biased. Note that CUFFEY's numbers for the uncontaminated, fresh bulk sample are in fairly good agreement with mine. Also note that in the surface collections, CUFFEY—being most interested in the RBR—found 69% (to my 11%) of RBR in his sample. On the other hand, being most interested in the DBR, I found 67% (to his 21%) of DBR.

A third point can also be made here. Paleontologists often treat the fauna of a thin rock unit as a whole, calculating the percentage of total fauna which each species present comprises (for example, as I did in Table 2). However, variations in the fauna at different stratigraphic levels within such units are desirable for some scientific purposes; such variations can be studied by collecting samples from successive horizons within a particular rock unit. In Table 3, I have tabulated the results of collecting this same unit (of Table 2) in successive thirds.

TABLE 3. *Vertical Distribution of Bryozoan Zoarial Growth Forms Within the Upper Havensville Calcareous Shale at Locality MS06. Fresh Samples from the Upper, Middle, and Lower Thirds of the 3-foot-thick Rock Unit Were Collected Separately, Processed Identically, and Then Completely Picked for Bryozoans.*

Upper Third: 280 Specimens

Zoarial Growth Form	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN
Numerical Abundance	00	09	00	43	21	00	16	191
Percent Abundance	00	03%	00	15%	07%	00	06%	68%

Middle Third: 184 Specimens

Zoarial Growth Form	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN
Numerical Abundance	00	01	01	84	41	01	00	56
Percent Abundance	00	TR	TR	46%	22%	TR	00	30%

Lower Third: 47 Specimens

Zoarial Growth Form	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN
Numerical Abundance	00	00	00	13	06	00	00	28
Percent Abundance	00	00	00	28%	13%	00	00	59%

Total Specimens = 511, all bfn PC.

Examination of this material yields an interesting conclusion. The percent of total fauna which a given form comprises in a sample collected from a unit bulk-sampled as a whole coincides with that form's percentage at various levels within the unit, not always with its percentage in the middle level of the unit. This differs from the belief expressed privately by some paleontologists that the middle level within a unit can often be regarded as a kind of "average" horizon for the unit as a whole. For

example, the percent of fauna which DBR comprises in the shale unit of Table 2 treated as a whole is 22%, which value is encountered only in the upper third of the unit. Again, RPI represents 14% of the fauna of the shale as a whole, and FEN 57% (Table 2); both these values are found in both the lower and the upper thirds of the unit, rather than in its middle third.

Consequently, it is evident that conclusions based upon data such as those presented in this section can be considered reliable only if they are drawn from fresh or uncontaminated samples taken from a number of outcrops. In particular, broad ecologic or stratigraphic interpretations based on single-outcrop weathered-free samples are highly suspect.

PROCESSING OF SAMPLES

The limestone and their included cherts were not treated further (except a few limestones which I dissolved in 10% acetic acid to examine their insoluble residues).

The siltstones and sandstones were mechanically disaggregated. Upon drying, these samples could be completely disaggregated by crumbling them between my fingers; never were more exertive measures required. After crumbling, the samples were dry-sieved by hand, with A.S.T.M. screens of 10, 20, 40, 60, and 80 meshes. This was done simply to facilitate micropaleontologic examination of the samples, and thus there is no significance attached to the particular sieve sizes used.

The shales and mudstones were broken up by the standard kerosene method. When disaggregation was not accomplished after following the kerosene procedure, Quaternary "0" (manufactured by Geigy Industrial Chemicals of Yonkers, New York), a powerful, slightly acid detergent, was employed. This technique was generally successful. If neither method effected disaggregation, the sample was reclassified as an argillaceous limestone and handled accordingly, but this was rare. After disaggregating them, the samples were sieved (wet) by using A.S.T.M. screens of 10, 20, 40, 60 and 120 mesh. These residues were appropriately labeled, placed in envelopes when dry, and stored for later sorting.

Before processing, either mechanical or chemical, a fresh, untreated portion of each sample was set aside. Then, this could be used later for palynological analysis or X-ray diffraction study or any other future process requiring uncontaminated samples.

All samples of fresh rock, sieved rock or rock prepared in any other way, are stored in the paleontological collections of The Pennsylvanian State University Department of Geology and Geophysics. Appended to each sample label is a statement of whether the sample was fossiliferous or unfossiliferous.

SAMPLE SORTING TECHNIQUES

Bryozoans were picked from samples in one of two ways—randomly or completely. When random sorting was used, I would pick, at random, bryozoans from the sample residues for not less than fifteen minutes nor more than twenty minutes. When complete sorting was used, I picked all the bryozoa from the 10- and 20-mesh sieves. Occasionally, because of the superabundance of fossil material, the 20-mesh screenings had to be split into quarters by using a microsplitter (Newton & Dutcher, 1970).

Having separated the bryozoa from the sample (randomly or completely), they were grouped according to zoarial growth forms. Cuffey (1966, 1967), the initiator of Wreford bryozoan studies utilizing some of the ideas of Stach (1935, 1936, 1937), devised the scheme used here by me (hopefully, future workers will work their collections into these divisions as well). I have already described briefly the eight zoarial growth forms found in the Wreford; elsewhere in this paper, the paleoecological importance of these growth forms is discussed (see also, Cuffey, 1966, 1967).

Sorting by growth form, which is based solely on the size and shape of individual bryozoan colonies, can be done rapidly, which is important, because no time is lost in trying to key out species. Wreford (indeed, Permian) bryozoans are but poorly known. Those which are known are subject to question and revision. The zoarial growth forms discussed here, in fact, often cut across taxonomic boundaries. An example of this is the zoarial growth form of encrusting sheetlike bryozoans. Included in this growth form are representatives of the Cryptostomata, Trepostomata, and Cyclostomata—three separate orders!

SPECIMEN PREPARATION METHODS

The study of cryptostome and trepostome bryozoans requires preparation of three sections for each zoarium—tangential, a shallow section parallel to the long axis of the zoarium; transverse, a section at right angles to the long axis of the colony; and longitudinal, a section parallel to and containing the zoarial axis. The necessity of preparing these sections, and the relative difficulty involved in their preparation, have resulted in two things. First, there are comparatively few workers on the bryozoans. Second, these few workers have made only very few studies with a sufficient number of bryozoan sections to have ever established a basis for the standardization of nomenclature. Also, because there are many Paleozoic bryozoans greater than one centimeter in diameter, the smaller genera (including the rhabdomesid cryptostomes), have been both poorly studied and poorly defined; this is due primarily to technological difficulties involved in cutting three sections from one specimen which is only one or two millimeters in diameter.

To overcome the two problems of specimen size and sample size, special techniques were developed and employed to prepare the Wreford rhabdomesids. To prepare approximately 1,000 specimens to yield three sections

each, normal thin-sectioning methods would have required at least 1,500 hours, an amount of time roughly equal to 200 eight-hour work days (assuming, of course, continuous labor). Consequently, I used acetate peels to markedly accelerate preparation of the rhabdomesids.

The basis of the technique which I used is discussed by BOARDMAN & UTGAARD (1964). Valuable instruction on refinements of that technique were given me by R. S. BOARDMAN (Curator of Invertebrate Paleontology, The United States National Museum, Smithsonian Institution) and his staff. Certain minor additional modifications were made by me as the work progressed.

Briefly, the method consists of placing the specimen into some transparent or translucent medium, then replicating selected surfaces of the specimen. (Below, in the detailed step-wise discussion, the step numbers, 1, 2, 3, 4, 5, and 9 also refer to Figure 6.)

1. Epotuf (Resin 37-128, Hardener 37-614, manufactured by the Reichold Chemical Company, Elizabeth, New Jersey), a clear yellowish epoxy, mixed four parts of resin to one part of hardener, is poured into a gelatin capsule of appropriate size till about one-half full. A label is then submerged, face downward, in the epoxy.

2. This should be placed in a drying oven with temperature preset between 35°C (95°F) and 40°C (102°F). From one and one-half to three hours is required for complete hardening of the epoxy. Epotuf will cure in about the same amount of time without this heat but will contain small bubbles as a consequence.

3. The specimen is now set atop the hardened epoxy. Care should be taken in placement if some precise orientation is required.

4. More epoxy is poured in. Just enough is added barely to cover the specimen.

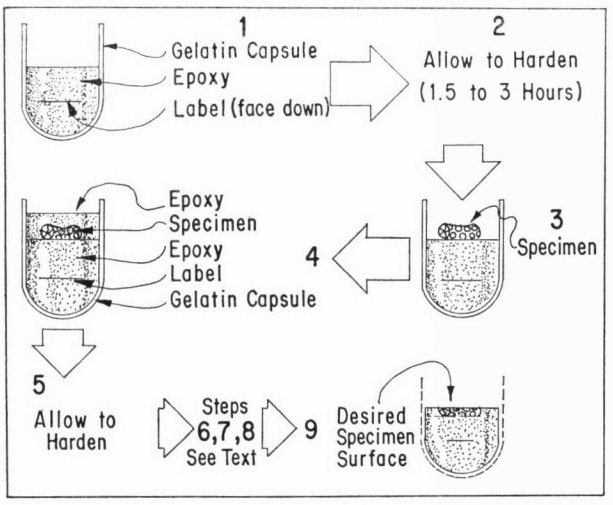


FIG. 6. Step-wise explanation of the specimen embedding technique employed in the preparation of thin sections and peels.

5. The hardening procedure is followed, as in Step 2 above.

6. When the upper layer of epoxy has hardened, the gelatin capsule with its contained epotuf-specimen-epotuf "sandwich" is put into warm water. The gelatin capsule dissolves, leaving only the sandwich.

7. Using coarse grit (600 or a little coarser), the epoxy overlying the specimen is ground away.

8. Switching to finer grit (1200 grit), the specimen is ground slowly down to the surface desired. Then, this surface is polished on 1500 grit (coarse polish), and finally with Bueller Microcloth. The specimen surface is then cleaned by brief immersion in an ultrasonic tank.

9. Figure 6 shows the condition of the epoxy pellet after the above eight steps. It is now ready for the replication procedure.

10. The polished surface is etched by plunging it into 1:20 acetic acid (or 1:20 formic acid) for about ten seconds.

11. This is then washed thoroughly and immediately in distilled water and allowed to dry completely; the preparator must be careful not to touch the etched surface.

12. Cellulose acetate, in 60 mill, cast, 21 × 50 × 0.060 inch sheets (available from the Plastics Division of Glass Distributors, Inc., Washington, D.C.) should previously have been cut with metal shears into one by three inch pieces. These will be microscope "slides." Using Pelikan Drawing Ink "K," all "slides" must be labelled to match the labels emplaced in the epoxy pellets.

13. The specimen surface is now flooded with acetone and placed immediately onto the cellulose acetate slide with a smooth, rolling motion, applying little or no pressure. Acetone *must* completely cover the specimen surface!

14. This is set aside and allowed to dry for several (five to ten) minutes.

15. The pellet is then removed from the slide with one abrupt snap. Any adhering fragments may be removed by brief immersion of 10% hydrochloric acid.

16. After removing the slide from the concentrated acid, the surface is washed quickly with distilled water, and then allowed to dry before storage.

Slides prepared this way in 1962 have as much detail now as when first made. On them, resolution is possible to 25 to 50 Angstroms. Since the purposes of most studies only require resolutions of a few microns, and since the practical limit of light microscopy is 1000 Angstroms (that is, 0.1 microns), this technique far exceeds all requirements for observation of fine detail.

Another advantage of the peel technique is that the preparator can make serial peels, at intervals of 0.01 millimeter. The speed at which such serial sectioning can be done far outstrips that possible with any other technique.

SYMBOLIZATION OF MORPHOLOGICAL PARAMETERS

In the text, plates, tables, figures, and appendices, the following symbols are employed. Wherever possible throughout this work, I have tried to continue CUFFEY's (1966, 1967) terminology. The symbols Z1, Z2, MZAD, IWT, and TP are all taken from his work. Because acanthopores are present as micracanthopores and megacanthopores in the cryptostomes and are perhaps not homologous to the acanthopores of the trepostomes, I have not used his symbolization for them.

Reference is made to these symbols throughout the text, and more complete discussions of each may be found in the appropriate portions of the text. I summarize and illustrate (Fig. 7) them all here, however, for the convenience of the reader:

ZA = The number of zooecial openings in a transverse section.

Z1 = The number of zooecial apertures observed in one square millimeter in a tangential section.

Z2 = The number of zooecial openings observed in two millimeters, measured parallel to branch axis in a longitudinal section.

MZAD = Maximum zooecial aperture distance, in millimeters, measured between adjacent zooecia.

IWT = Interapertural wall thickness, in millimeters.

TP = Thickness of the peripheral region as measured in the longitudinal section, in millimeters.

DTZ_2 = Total number of diaphragms observed in two millimeters measured parallel to branch axis in the longitudinal section.

NIHS = Total number of inferior hemisepta in two millimeters measured parallel to branch axis in the longitudinal section.

NSHS = Total number of superior hemisepta in two millimeters measured parallel to branch axis in the longitudinal section.

MMSP = Maximum width of the mesopores, in millimeters.

MMAW = Maximum megacanthopore diameter, in millimeters.

MMUW = Maximum micracanthopore diameter, in millimeters.

MNUW = Maximum number of micracanthopores observed between two megacanthopores within one square millimeter.

NRIW = Maximum number of rows of micracanthopores observed in an interapertural space.

NMA = Number of megacanthopores in one square millimeter.

NMU = Number of micracanthopores in one square millimeter.

NMSP = The number of mesopores in one square millimeter.

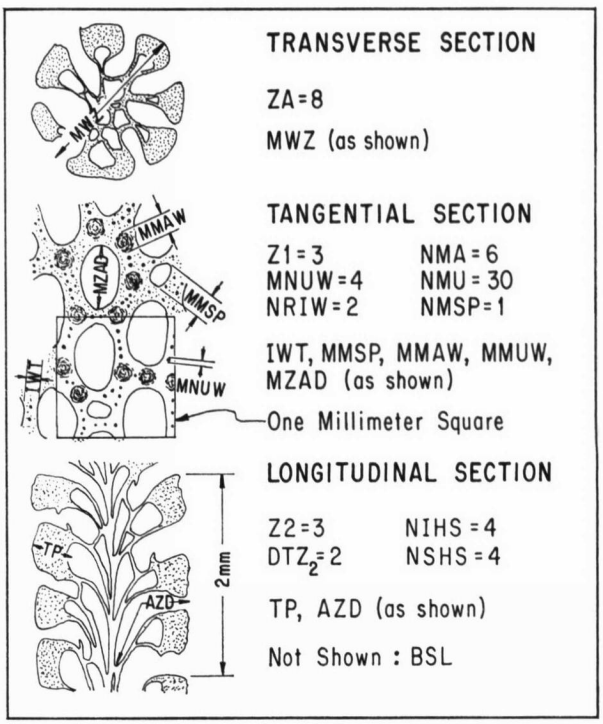


FIG. 7. Morphological features and their symbolization used in the assessment of the Wreford Rhabdomesidae.

MWZ = Maximum width of the zoarium, in millimeters.

AZD = Average zooecial depth, measured axially in the longitudinal section, in millimeters.

BSL = Thickness of the basal lamina, in millimeters.

Some further discussion for a few of the parameters outlined above seems necessary, firstly because CUFFEY (1966, 1967) measured some of the same parameters and secondly because ANSTEY and PERRY (1970) have suggested measurements for these features but in a different fashion. During the discussion below, reference to Figure 7 will help the reader visualize the morphologic relationships involved.

IWT is measured transversely between zooecial openings at the minimum point of separation in the interzooecial space.

Z1 is meristic. First, the total number of *entire* zooecial apertures is counted. Next, the number of apertures partially within the one square millimeter is totalled separately, and expressed in terms of the number of entire zooecial apertures to which they collectively are equivalent. Then, the number of entire zooecial openings is added to the number of zooecia made up of portions, and this total is the number reported as Z1. As an example, in Figure 7, the Z1 value is three. One entire aperture plus two nearly complete apertures plus minor portions of three others are added for a total of three.

Z2 is also meristic. This is generated by starting with a zooecial opening and measuring two millimeters along the outside of the section, parallel to the long axis of the zoarium. Only complete zooecia are counted; thus Z2 is always a whole number.

NMSP, NMA, NMU are counted much as Z1. That is, the number of entire elements (mesopores, megacanthopores or micracanthopores) is counted and the partial elements totalled are then added on.

NRIW is generated by viewing the surface of the entire tangential section. Whatever the highest value observed, it is recorded as NRIW. Since the micracanthopores are such shallow, near-surface features, their meristic evaluation is highly variable, and depends upon the depth of section. In addition, since these tangential sections are of very small cylindrical branches, this value is better evaluated by viewing the entire surface. The same procedure for the same reasoning is used in evaluation of MNUW.

NIHS, NSHS, and DTZ_2 are observed by first making the Z2 measurement, then making the counts, on only one side of the zoarium (in longitudinal section), within the two-millimeter distance used for the Z2 observation. This is done so that the Z2 value has more meaning relative to DTZ_2, NSHS and NIHS than it otherwise might have. That is, from measurements like $DTZ_2 = 5$ and $Z2 = 5$, it can be inferred that this specimen has one diaphragm in each zooecium.

AZD, as Figure 7 tries to convey, is measured axially, in linear segments, in the center of the zooecial tube. Viewing the longitudinal section as a whole, two zooecia are selected as "average" ("typical" of the section) insofar as depth, width of opening, number of diaphragms, etc., are concerned. Both are then measured, the average of the two being entered as AZD in the tabulations for that zooarium.

TP is measured, as Figure 7 shows, orthogonally to the growth laminae and represents the thickness of the outer, laminated skeleton.

SPECIMEN-LABEL SYMBOLIZATION

Certain other symbols are appended to every specimen and to every suite or group of specimens. These appear after the locality and horizon symbols and are as follows:

bfN = Specimen(s) taken from a bulk fresh sample, by myself (the "N" indicates NEWTON in all cases).

bf = Specimen(s) taken as above, but by CUFFEY.

ppN = Samples picked in place from the surface of the outcropping unit.

float or S = Samples picked from float or surface wash.

bsf = A mixture of surface and fresh material collected together in one bulk sample.

PC = Every bryozoan was picked completely from the screenings.

PR = Bryozoans were picked randomly from the screenings.

Examples:

GR01E m ⅓ bfN PC. This means all the bryozoans (PC) were taken from a bulk sample of the fresh material collected by me (bfN). The sample came from the middle third (m ⅓) of the Eth bed (E; here E is the Upper Speiser Calcareous Shale) from locality 01 in Greenwood County, Kansas (GR01).

OS02C float. This means that the bryozoa were picked up as float from bed C, locality 02, Osage County, Oklahoma.

ANALYSIS OF DATA

GENERAL CONSIDERATIONS

Two concerns were foremost in my handling of the data gathered in this study. First, whatever treatment I selected must be consistent with that of previous workers (for example, CUFFEY, 1966, 1967; FOERSTER, 1970; HOROWITZ, 1968) and must be of a straightforward (that is, easily reproducible) nature. Second, whatever methods chosen must utilize all or nearly all of the data available.

The first was satisfied by using the straightforward and well-known statistics of mean, median, mode, standard deviation, skewness, kurtosis, and coefficient of variation.

The second was necessitated by the guiding consideration of this paper; namely that this work is the first thorough consideration of ramose cryptostome bryozoans. Some techniques, such as factor analysis, would have reduced the number of parameters needed to account for most of the variability, and smaller sample sizes would have reduced the amount of time spent in data gathering. Those few parameters necessary to account for most of the observed morphologic variability among the Wreford rhabdomesids would be useful in constructing diagnostic keys for identifying the Wreford bryozoan species, a task which will eventually be undertaken after all the species involved have been described. Those few parameters would, however, by themselves be woefully inadequate for the thorough understanding of morphologic variability which is a necessary prerequisite for the future development of a soundly based bryozoan systematics. Furthermore, I hope that this paper will serve as a guideline and stimulus for future cryptostome studies; consequently, it should be as complete as possible in its coverage. Finally, morphologic characters, which seem unimportant among the Wreford rhabdomesids may be quite important in accounting for the variability yet to be found in other cryptostome groups; again, this possibility implies to me that this study should encompass all possible morphologic variations available for observation.

STATISTICAL TREATMENT METHOD

All statistics were computed by the IBM System

360/67 computer of The Pennsylvanian State University Computation Center. On record at the Center are numerous "library programs." These programs enable users to call certain other programs to operate upon their data. Two programs from this library were utilized in this phase of the study: NORM and the STPAC program STSUM.

NORM is the name of the library program which computes frequency polygons, statistics, and moments for one variable. The statistics computed are; mean, standard error of mean, standard deviation, variance, coefficient of variation, root beta 1, root beta 2.

As compile time, and thus cost, was high for NORM, most of the data was run under the subprogram STSUM of STPAC. STPAC (the program name abbreviated from "statistical package") is composed of two segments, a monitor and a set of statistical programs. The program of this set of programs that I used was STSUM (statistical summary), which can handle up to 105 variables and an unlimited number of cases for each variable. Statistics computed include those mentioned above under NORM, plus sample size, skewness, and kurtosis.

The tables of Appendix B summarize all the statistical output from the operation of these programs upon the Wreford rhabdomesid data.

CLUSTER ANALYSIS

Because of the inherent difficulties involved in comparing many characteristics across many samples, a method called "cluster analysis" was employed. Basically, the program is a modification of that used by Bonham-Carter (1967). Some alteration was required to run this program on The Pennsylvanian State University IBM System 360/67.

The twenty parameters used in the analysis of the Wreford Rhabdomesidae were coded in the following manner for use in cluster analysis. First, the statistics for each parameter were computed; then the distribution was divided into five classes. These five classes were coded into two-state form in this way: Class 1, 1111; Class 2, 1112; Class 3, 1122; Class 4, 1222; Class 5, 2222. Note that each class differs from the classes which precede and follow it by one number, which are above or below it by two numbers. Thus, at the ends, Class 1 differs from Class 5 by all four numbers. That is, as one ascends the number of classes, the degree of difference increases. The original class data is now ranked into progressively dissimilar groups.

The clustering method used by Bonham-Carter in this program is a pairing, iterative process, fully described by Sokal & Sneath (1963).

The data matrix utilized in this study of Wreford rhabdomesids is 544 (samples) by 80 (characters). Output from this was not drafted into a dendrogram by me because of its enormous size. However, I randomly selected a 200 by 80 matrix from the larger one. The printout from this program (200 by 80) was interpreted into a dendrogram by me and is Figure 9. The matrix of coefficients of association for the 544 by 80 matrix is on file in the Paleobryozoological Research section of the Department of Geology and Geophysics of The Pennsylvania State University. The interpretation of this dendrogram is discussed later when considering the variability of the Wreford Rhabdomesidae. This cluster-analysis program is also used in this paper to investigate the family Rhabdomesidae as a whole. In addition, a work in progress will use this program to attempt a classification of the Cyclostomata (Cuffey, Thorn, Newton, and Utgaard, in preparation).

It must be kept in mind that this cluster analysis by itself does not yield a modern systematic taxonomy, but rather a simple numerical pheneticism or numerical classification scheme termed "numerical taxonomy" by Sokal & Sneath (1963) (also see the remarks in Mayr, 1969, p. 68-69, 208-210).

SYSTEMATIC ANALYSIS OF WREFORD RHABDOMESIDAE

PHYLA

In recent years, most bryozoans have been referred to either the phylum Ectoprocta or the phylum Bryozoa. These two phylum concepts are not synonymous, and much controversy exists concerning them. At least eight articles in the last ten years have discussed this point, terminating, one hopes, with Cuffey (1969). "Ectoprocta" refers only to the eucoelomate, lophophorate colonial organisms of the groups Ctenostomata, Cheilostomata, Cyclostomata, Cystoporata, Trepostomata, Cryptostomata, and Phylactolaemata. "Bryozoa" refers to Ectoprocta plus Entoprocta.

Following the usage urged by Schopf (1967, p. 277) and Cuffey (1967, p. 40; 1969, p. 251), I will use Bryozoa to denote Ectoprocta plus Entoprocta, so that "rhabdomesid cryptostome bryozoans" is equivalent to, but somewhat less precise than, "rhabdomesid cryptostome ectoprocts." The informal term "bryozoan" will be used almost exclusively throughout this paper, however, in line with these previous worker's suggestions.

ORDERS

Of the five presently recognized Paleozoic bryozoan orders (Ctenostomata, Cyclostomata, Cystoparata, Trepo-

stomata, Cryptostomata) only two, the trepostomes and cryptostomes, are well known to most paleontologists. Such names as "stony bryozoa" (an unfortunate appellation), "ramose bryozoa," and "twig-like bryozoa" are found in common use regarding these two groups.

At present, much confusion exists as to what the differences are between Trepostomata and the Cryptostomata. Of the Cryptostomata, HYMAN (1959, p. 395) said, "This order . . . does not appear to differ in any important respect from the [Trepostomata]." Further, she states (HYMAN, 1959, p. 395), "The main difference [of cryptostomes] from trepostomes consists in the presence of a long tube between the external opening and the distal hemiseptum." This might be considered acceptable; however, most cryptostome genera lack hemisepta.

BASSLER (1953, p. *G*22) briefly defines the Trepostomata as possessing "zooecial tubes with distinct immature and mature regions, aperture terminal." Of the Cryptostomata, he says, "like Trepostomata but immature region short, aperture at bottom of vestibule."

In their text, MOORE, LALICKER, & FISCHER (1952, p. 161) supply these differences:

"Trepostomata (order), animals enclosed by a long curved calcareous tube, generally intersected by partitions. Immature and mature parts of the colonial structure are distinct . . . Cryptostomata (order), animals enclosed in a relatively short calcareous tube, walls near the periphery of the colony much thickened."

BASSLER (1953, p. *G*90) describes the Trepostomata more fully as follows:

"Zooecia consist of long calcareous tubes, generally intersected by many partitions (diaphragms), each tube being divisible into an immature region in the axial part of the zoarium characterized by thin walls, wide spacing of diaphragms, and contact with other zooecia on all sides, and a mature region near the zoarial surface characterized by thickened walls, close spacing of diaphragms, and intervention of special cells (mesopores, acanthopores) between zooecia."

For the Cryptostomata, BASSLER (1953, p. *G*119) offers this description:

"Zooecia as in Trepostomata, with well-marked differentiation of immature and mature regions, but the boundary between them more abrupt and the tubes much shorter; the distal part of each zooecial tube is a vestibule that extends from the aperture at the surface to the position of the orifice near the inner boundary of the mature zone, defined in many forms by shelflike hemisepta projecting from the walls. Interspaces between adjacent vestibules commonly filled by vesiculose coenosteum or solid stereoem, which may be traversed by acanthopores."

On the other hand, after reading these statements and others (see BOARDMAN & CHEETHAM, 1969), and by examining numerous bryozoan thin sections, one is instead drawn to the conclusion that there are no clear-cut differences; the two orders are *not* distinct. Moreover, the new Paleozoic order Cystoporata (ASTROVA, 1964) and the long established order Cyclostomata seem confusingly similar to each other; happily, the need for extensive revision of bryozoan ordinal concepts is widely recognized by bryozoan workers.

CRYPTOSTOME FAMILIES

Within the order Cryptostomata VINE, 1883, several distinct groupings of bryozoans can be recognized. Traditionally (BASSLER, 1953, p. *G*120-147), the Cryptostomata has been divided into twelve families. By present standards, these families are poorly diagnosed and neither readily nor uniquely distinguishable.

However, by grouping the cryptostomes on the basis of a few distinct characteristics, six tidy taxa can be generated. I therefore suggest, informally, an improved arrangement for familial-rank taxonomy among the cryptostomes. The definitions given here are not intended to be exhaustive, but rather only to convey the basic or classificatory characteristics for each taxon. Later in this paper, I will discuss one of these families, the trepostome-like Rhabdomesidae, more fully. Four groups (Fenestelidae, Acanthocladiidae, Arthrostylidae, and Rhabdomesidae) are the same as in BASSLER (1953). The other two are new groupings of forms previously separated as distinct at the familial level, although both bear previously published names used in expanded sense:

Fenestellidae: These are zoaria with non-zooeciate dissepiments joining erect zooecia-bearing branches. Commonly, though not necessarily, they bear acanthopores (as spines) and hemisepta (usually superior). They are commonly heavily sclerenchymatous and are generally without mesopores.

Ptilodictyidae (expanded): This group could be termed the "planar" family of cryptostomes; it is composed of the Stictoporellidae, Rhinidictyidae, Sulcoretoporidae, Rhinoporidae, and Ptilodictyidae of BASSLER (1953, p. *G*136-*G*137, *G*142-*G*143) and earlier writers. These ectoprocts are bifoliate or unilaminar, or rarely trilaminar or trifoliate. Mesopores are rare. Monticules and maculae are commonly developed. A median or basal plane is present, with or without tubuli. Most commonly these form colonies which are bifoliate branches with or without articulation points. Hemisepta and lunaria are common. Acanthopores are generally absent.

Paleschariidae (expanded): This group consists of the so-called cheilostome-like families Worthenoporidae, Cycloporidae, and Paleschariidae of BASSLER (1953, p. *G*144-*G*147). (The Actinotrypidae have been removed from the cryptostomes to the fistuliporoids by HOROWITZ (1968). These bryozoans are characterized by having semi-elliptical zooecial apertures, commonly surrounded by projecting elements.

Acanthocladiidae: This family, as is the Fenestellidae, seems to be a very natural grouping. The zoaria are comprised of stout, central axes from which obliquely project branching and rebranching zooeciate elements. These branches may be united by dissepimental structures, as in the Fenestellidae, but the dissepiments are zooecia-bearing, unlike the Fenestellidae.

Arthrostylidae: These zoaria are cylindrical (rarely)

or subcylindrical (usually). They are comprised of dichotomously branching articulated segments. Zooecial apertures exist on one side of the zoarium (most common) or, if on all sides of zoarium, are spirally deployed about a central axis.

Rhabdomesidae: The characteristics of this family are very trepostome-like with several exceptions. First, the peripheral or mature zone's zooecial walls are four to ten or more times the thickness of the inner or immature zooecial walls. Second, the cross-sectional cavity of the zooecial tube at the base of this thickened zone (adaxially) is referred to as the **aperture**; the portion extending abaxially away is labeled the **vestibule**, and the external opening of the zooecial tube is the **zooecial opening.** Third, commonly there are two sizes of acanthopores; megacanthopores and micracanthopores. These acanthopores, when present, are restricted to the mature zone; that is, they do not extend into the axis. Hemisepta are common. Mesopores are rare and are not crossed by numerous diaphragms as in the trepostomes. Diaphragms are complete and, when developed at all, scarce and scattered in the zoarium.

FAMILY RHABDOMESIDAE

For formal taxonomic purposes, the name of this family can be given as follows: Family RHABDOMESIDAE Vine, 1883 (*nom. corr.* Bassler, 1953, *pro* Rhabdomesontidae) (= Rhomboporidae Simpson, 1895: Bactroporidae Simpson, 1897).

Along with the Fenestellidae, the Rhabdomesidae are the most common of the cryptostome ectoprocts. The Order Cryptostomata contains approximately 135 genera distributed among several families. Of these families the Fenestellidae (with 30 genera) and the Rhabdomesidae (with 31 genera) are the most conspicuous elements among Paleozoic cryptostome assemblages.

The Rhabdomesidae have a stratigraphic range of Ordovician to Permian. The oldest known rhabdomesid is *Nematotrypa gracilis* Bassler, 1911, from the Echinospherites Limestone (middle Upper Champlainian = Llanvirnian-Llandeilian) of Reval, Estonia. The youngest known are *Streblascopora delicatula* Sakagami, 1961, and *Hayasakopora matsudae* Sakagami, 1961, from the Iwaizaki Limestone (Leonardian-Guadalupian = *Parafusulina*) of North Honshu, Japan.

The 31 rhabdomesid genera, arranged alphabetically, are these:

1. *Acanthoclema*
2. *Ascopora*
3. *Bactropora*
4. *Claustotrypa*
5. *Coeloconus*
6. *Goldfussitrypa*
7. *Hayasakopora*
8. *Hyalotoechus*
9. *Hyphasmopora*
10. *Idioclema*

Table 4. *A Listing of the Rhabdomesid Cryptostomes.*

	Saffordotaxis 0011 11	*Hayasakopora 0010 11*	*Coeloconus 0110 11*
Permian	*Rhombopora 0011 11*	*Streblascopora 0010 1/11*	*Rhabdomeson 0110 11*
NOT: 0	*Clausotrypa 0011 11*	*Streblocladia 0010 1/11*	
	Clausotrypa 0011	*Rhombopora 0010 //*	*Coeloconus 0110 //*
Pennsylvanian	*Saffordotaxis 0011 //*		*Rhabdomeson 0110 //*
NOT: 6	*Rhomboporella 0011 1/11*	*Hayasakopora 0010 1*	
	Megacanthopora 0011 1/11		
	Acanthoclema 0011 11		
	Saffordotaxis 0011 1	*Rhombopora 1111 //*	*Coeloconus 0110 1*
Mississippian	*Acanthoclema 0011 //*	*Rhombopora 0001 //*	*Rhabdomeson 0110 1*
NOT: 7	*Clausotrypa 0011 1*		*Idioclema 0110 1/11*
	Bactropora 0011 11		
	Linotaxis 0011 1/11	*Hyalotoechus 1110 1/11*	
	Petaloporella 0011 1/11	*Nemataxis 1110 1/11*	
Devonian	*Acanthoclema 0011 1*		
NOT: 3	*Bactropora 0011 1*		
	Rhombopora 0011 1	*Orthopora 1110 11*	
Silurian		*Orthopora 1110 1*	
NOT: 1			
	Goldfussitrypa 0011 1/11	*Ottoseetaxis 0010 1/11*	
Ordovician		*Nemataxidra 0010 1/11*	
NOT: 0 (?)	*Nematotrypa 1110 1/11*		

KEY: 1 = First appearance of taxon; 11 = Last occurrence; 1/11 = First and last occurrence of same age; // = Mid-range occurrence; NOT = Number of on-going taxa. Numerical symbols in text.

11. *Linotaxis*
12. *Megacanthopora*
13. *Nemataxis*
14. *Nemataxidra*
15. *Nematotrypa*
16. *Nicklesopora*
17. *Orthopora*
18. *Ottoseetaxis*
19. *Petaloporella*
20. *Rhabdomeson* (*R. gracile* is type of genus)
21. *Rhombocladia*
22. *Rhombopora*
23. *Rhomboporella*
24. *Saffordotaxis*
25. *Spirillopora*
26. *Streblascopora*
27. *Streblocladia*
28. *Streblotrypa*
29. *Streblotrypella*
30. *Syringoclemis*
31. *Tropidopora*

In Table 4, I have arranged the family phylogenetically, based on four easily observed characteristics. These four were selected because, even in older works and poor figurative reproductions of any age, their presence or absence can always be determined. Also, again, in older publications (and, alas, in some recent ones), scales are vague, imprecise, or lacking; consequently, measurements are impossible to know except in the rare cases when supplied in the accompanying text.

In Table 4, there appear four numbers following each generic name. Each number, either a zero or one, indicates the presence ("1") of a structure or its absence ("0"). These four structures are, in order, inferior hemisepta, superior hemisepta, acanthopores, and diaphragms. Thus, the listing, "*Bactropora* 0011," means that the genus *Bactropora* has no hemisepta (either inferior or superior) but does have acanthopores and diaphragms.

Bassler (1953), p. *G*129-*G*136 classifies the rhabdomesid genera on the basis of seven characters. I tested the consistency of his classification by utilizing these seven characters as two-state, present-absent data. The cluster program written by Bonham-Carter (Bonham-Carter, 1967) was modified by me to run on The Pennsylvania State University IBM 360/67 computer. Presence was coded as "1," absence as "2." Table 5 presents Bassler's seven characters and the coding which I assigned to them. Next, each of Bassler's generic descriptions, augmented by an analysis of his illustrations for each genus, was coded into this two-state system.

Table 5. *Character-state Coding for the Two-state Analysis of the Family Rhabdomesidae, as Used for the Cluster Analysis of its Component Genera.*

Character	Coding:	1	2
1. Colony		branched	unbranched
2. Axis of colony		not hollow	hollow
3. Diaphragms		present	absent
4. Hemisepta		present	absent
5. Megacanthopores		present	absent
6. Micracanthopores		present	absent
7. Mesopores		present	absent

Figure 8 is the dendrogram produced by a cluster analysis of these codings. For three of the genera, insufficient information was given by Bassler to enable coding of all seven characters. For 26 genera, information on all seven parameters was presented, and the dendrogram of Figure 8 is produced from this 26 x 7 matrix.

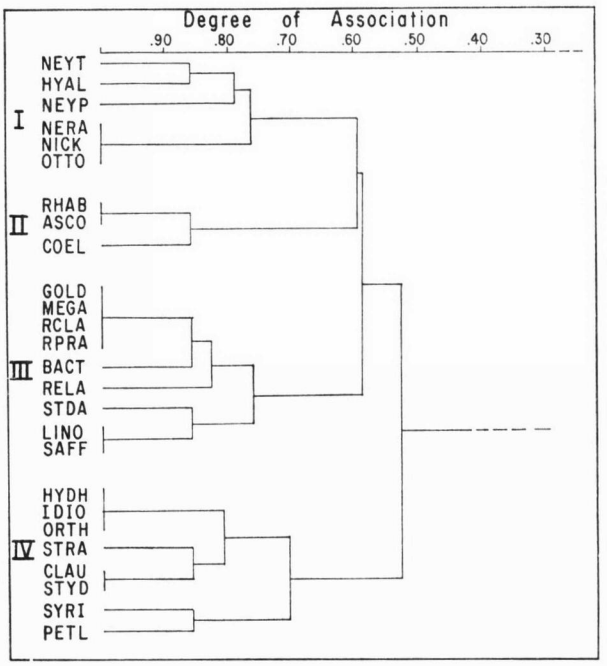


Fig. 8. Dendrogram of the genera of the family Rhabdomesidae based on the seven classificatory characters used by Bassler (1953).

The four-letter designations for the genera are explained in Table 6. Also, in Table 6, I present the original data matrix—the "raw data" for the dendrogram computations. Four groups, I-IV are generated by the above technique. Group 1 is characterized by having no diaphragms or mesopores and some have no megacanthopores. Group II, the smallest grouping, has a basal lamina (= hollow axis). Group III has megacanthopores, micracanthopores and diaphragms. Group IV has mesopores and hemisepta. Group 1 agrees internally at the .7619 level of association, Group II at .8517, Group III at .7619, and Group IV at the .7143 level. Group I clusters with Group II at the .5952 level, this grouping clusters in turn with Group III at the .5873 level, and finally Group IV is joined with the others in the cluster at the .5198 level. More comments on the clustering method are offered below, and also by Bonham-Carter (1967).

Because so few characters are available for use in constructing the clusters, these particular clusters can only be used to suggest that there may possibly be natural subfamilial groupings among the rhabdomesid genera. It would be inappropriate at this time to propose here formal subfamilies for these fossils. Hopefully, future crypto-

TABLE 6. *Summary of the Two-state Coding for Genera of the Family Rhabdomesidae (characters from Bassler (1953)), as Used for the Cluster Analysis of Those Genera.*

GENUS	CHARACTER	ABBREVIATION
Rhabdomeson	1 2 2 2 1 1 2	RHAB
Ascopora	1 2 2 2 1 1 2	ASCO
Bactropora	2 1 1 2 1 1 2	BACT
Clausotrypa	1 1 2 1 1 2 1	CLAU
Coeloconus	2 2 2 2 1 1 2	COEL
Goldfussitrypa	1 1 1 2 1 1 2	GOLD
Hyalotoechus	1 1 2 1 1 1 2	HYAL
Hyphasmopora	1 1 2 1 1 2 2	HYPH
Idioclema	1 1 2 1 1 2 2	IDIO
Linotaxis	1 1 1 2 1 2 2	LINO
Megacanthopora	1 1 1 2 1 1 2	MEGA
Nemataxis	1 1 2 1 2 1 2	NEYT
Nemataxidra	1 1 2 2 2 1 2	NERA
Nematotrypa	1 1 2 1 2 1 1	NEYP
Nicklesopora	1 1 2 2 2 1 2	NICK
Orthopora	1 1 2 1 1 2 2	ORTH
Ottoseetaxis	1 1 2 2 2 1 2	OTTO
Petaloporella	1 1 2 2 1 2 1	PETL
Rhombocladia	1 1 1 2 1 1 2	RCLA
Rhombopora	1 1 1 2 1 1 2	RPRA
Rhomboporella	1 1 1 1 1 1 2	RELA
Saffordotaxis	1 1 1 2 1 2 2	SAFF
Streblascopora	1 2 2 1 1 2 1	STRA
Streblocladia	1 1 1 2 2 2 2	STDA
Streblotrypa	1 1 2 1 1 2 1	STYP
Syringoclemis	1 2 2 2 1 2 1	SYRI

stome workers will generate more comprehensive morphologic descriptions of these forms, so that the cluster-analysis technique demonstrated above can aid significantly in formulating a better classification of cryptostomes. Such comprehensive descriptions will probably emerge from the reexamination of rhabdomesid type materials being carried out for the revision of the bryozoan volume of the *Treatise on Invertebrate Paleontology* (D. B. BLAKE, personal communication, 1969).

In Appendix C, I have listed all the genera of the family Rhabdomesidae, along with all their species known to me. Following the genus name is the name of the type-species of the genus and the original designation. After each species' name is the geologic/stratigraphic position of its first description and, finally, the geographic locality of first description.

RHABDOMESID GENERIC CONCEPTS APPLICABLE TO WREFORD BRYOZOANS

Thirteen of BASSLER's (1953) 29 genera of rhabdomesid cryptostomes resemble *Rhombopora* enough that they are either compared by him to *Rhombopora* or have been split off from *Rhombopora*. In particular, the three genera *Rhabdomeson* YOUNG & YOUNG, 1874, *Saffordotaxis* BASSLER, 1952, and *Nicklesopora* BASSLER, 1952, very closely resemble *Rhombopora* MEEK, 1872, which is the earliest described genus in this family.

As discussed later in this paper, the Wreford rhabdomesids fall into two well-defined groups, interpretable as the two species *Rhombopora lepidodendroides* MEEK, 1872, and *Syringoclemis wrefordensis* NEWTON, n. sp. No formal taxonomic reference to any genus other than *Rhombopora* has ever been published for the rhabdomesids of the Wreford Megacyclothem. However, evidence from the Wreford rhabdomesids suggests that the three above-mentioned rhabdomesid genera are so similar to *Rhombopora* that they cannot in practice be distinguished from that genus. Consequently, this evidence implies that these three genera—*Rhabdomeson, Saffordotaxis,* and *Nicklesopora*—are better regarded as synonyms of *Rhombopora* than as distinct taxa.

First, however, some members of the Wreford population of *Rhombopora lepidodendroides* could possibly be referred to the genera *Rhabdomeson, Saffordotaxis,* or *Nicklesopora,* by workers unfamiliar with the extent to which this species varies morphologically within these rocks. In view of this situation, therefore, it seems evident that these three are faulty generic concepts.

Second, in addition to the foregoing reason, synonymizing these genera is also strongly supported by consideration of the relative insignificance of the traditionally recognized morphologic differences between these forms and *Rhombopora.*

Rhabdomeson differs from *Rhombopora* only by the presence of "a hollow axial epithecate tube from which zooecia extend" (BASSLER, 1953, p. *G*131). Plate 1, figures 10-12 show a complete gradational series from *Rhombopora lepidodendroides* MEEK overgrowing a brachiopod spine, to *R. lepidodendroides* MEEK overgrowing partially dissolved spines, to, finally, a specimen of *R. lepidodendroides* MEEK retaining only the axial basal lamina. This last mentioned configuration could occur one of three ways. First, this could be the form taken by the colony in the course of its growth from the ancestrula; this, of course, is the implication of the concept *Rhabdomeson.* However, because this frail, hollow cylinder seems far too fragile to survive any environmental rigors, I suggest that the concept *Rhabdomeson* is biologically untenable. Second, this could be the result of a *Rhombopora* ancestrula's encrusting a rigid, cylindrical body (such as an echinoid or brachiopod spine), which subsequently was dissolved or broken away; this removal could occur either predepositionally or diagenetically. Many examples of this process are apparently present in the specimens sectioned by me. Third, a *Rhombopora* ancestrula could have started out on the surface of a cylindrical algal frond. After completing the encrustration of the algal frond, the bryozoan would thus effectively prevent light from reaching the algal frond, consequently killing it. Or, the

weight of the bryozoan could have toppled the algal frond-bryozoan colony combination into the mud, killing both. In any case, the algal frond would not be preserved, since only the hard parts of the bryozoan colony would survive burial and fossilization.

In addition to the foregoing considerations, which suggest that *Rhabdomeson* is simply a *Rhombopora* growing on a particular substrate (a narrow cylindrical one), remember that *Rhabdomeson* differs from *Rhombopora* in only one morphologic character, and thus is a monothetic taxon. In general, single-character differences are insufficient basis for erection of generic taxa; no evidence exists which suggests that *Rhabdomeson* should constitute an exception to the general undesirability of monothetically-based taxa.

ELIAS (1957) elected to solve the *Rhombopora* versus *Rhabdomeson* question by erecting "*Rhabdomeson (Rhombopora)* as a phyletic sub-genus" which is "morphologically transitional between . . . *Rhabdomeson* and *Rhombopora* . . . the axial tube is present in some parts but never in all" (ELIAS, 1957, p. 401). He erects three species under this scheme; *Rhabdomeson (Rhombopora) rogersi, R. (R.) foerstei* and *R. (R.) ulrichi.* I consider them to be species of *Rhombopora* for the reasons stated above.

Nicklesopora is defined in the type description (BASSLER, 1952, p. 384, no figures) as being a "*Rhombopora* with a single row of micracanthopores around each zooecium." Also, it lacks diaphragms, hemisepta and mesopores.

Saffordotaxis in the type description (BASSLER, 1952, p. 385, no figures) is defined as being "like *Nicklesopora,* but one or two rows of megacanthopores surround each zooecium."

The preceding two paragraphs are the complete type descriptions (except for the designation of type-species and localities). No specimens are cited, none is illustrated. BASSLER's own definitive difference between megacanthopores and micracanthopores is one of degree or contrast only; that is, micracanthopores are "small . . . acanthopores associated with much enlarged ones (megacanthopores). . . ." (BASSLER, 1953, p. 12). Consequently, it seems impossible that a bryozoan could have micracanthopores only.

In Plate 2, figures 2-4, I have illustrated a series of tangential sections showing the gamut from extremely marked contrast between megacanthopores and micracanthopores, to virtually no contrast between the two. Since there is no other observable difference between typical Wreford (and other) specimens of *Rhombopora lepidodendroides* and these specimens, which on BASSLER's bases might be considered as referrable to *Saffordotaxis* or *Nicklesopora,* I conclude that all these specimens must be (other than *Syringoclemis*) referred to *Rhombopora.*

Syringoclemis is one of the the monotypic genera of the Rhabdomesidae. Only the species *Syringoclemis biserialis* GIRTY, 1911, is known to me, except for the examples in the Wreford Megacyclothem.

GIRTY 1911 did not figure any specimens of *Syringoclemis biserialis,* and did not designate any types. BASSLER (1941) figures some sections (as drawings), but states that GIRTY's types are unknown. BASSLER (1953) again figured some sections (the same drawings as used in the 1941 paper) and made no statement about type specimens. Also, I know of no species that have been assigned to this genus. No type *Syringoclemis* specimens are deposited at the United States National Museum, Smithsonian Institution (BOARDMAN, personal communication, 1969). Only the written description, therefore, was available to me for comparison with my specimens from the Wreford Megacyclothem. *Syringoclemis biserialis* GIRTY is defined thusly (GIRTY, 1911, p. 206-207):

". . . acanthopores scantily developed, of two sizes in the typical species . . . mesopores are confined to the cortical zone . . . branches . . . a diameter of 5 mm. or less. The zoarium itself is less than 1 mm. in thickness and lined with an epitheca . . . apertures . . . .18 to .21 mm. in longest diameter, rarely .28 mm, irregularly arranged and rarely in contact . . . Mesopores, irregular in size and arrangement. The largest are about half the diameter of the zooecia . . . six or less of the zooecia . . . occur in 2 mm. . . . considerable areas occur in which no acanthopores can be seen at all . . . mature region: .14 to .28 mm. . . . Tabulae, so far as observed, are entirely lacking both in the zooecia and the mesopores."

GIRTY's (1911) specimens came from the Fayetteville Shale (Upper Mississipian, Chester) of Arkansas. The two papers by BASSLER (1941, 1953) were discussions of GIRTY's specimens and did not add to the original range. Thus, this paper is only the second reference to the stratigraphic distribution of the genus, and extends the range of *Syringoclemis* into the Lower Permian (Council Grove-Chase).

SYNONYMY AND STRATIGRAPHIC RANGE OF RHOMBOPORA LEPIDODENDROIDES

As more fully discussed elsewhere in this paper, the most abundant Wreford rhabdomesid species is *Rhombopora lepidodendroides.* A complete synonymy for that species follows:

Rhombopora lepidodendroides MEEK, 1872

1872 MEEK, House Exec. Doc., United States 1st Session, 42nd Congress, p. 141-143, pl. 7, fig. 2a-2f.

1888 KEYES, Proc. Acad., Nat. Sci. Philadelphia, p. 225.

1894 KEYES, Missouri Geological Survey, v. 5, p. 35, pl. 33, fig. 4a, b.

1896 SMITH, Proc. Amer. Phil. Soc., v. 35, p. 237.

1900 NICKLES & BASSLER, U.S.G.S., Bull. 137, p. 395.

1901 ROGERS, Kansas Univ. Quart., v. 9, n. 4, p. 240, 241, 245.

1903 CONDRA, Nebraska Geol. Survey, v. 2, pt. 1, p. 99, pl. 6, fig. 2-4, p. 7, fig. 1-12.

1903 CONDRA, Am. Geologist, v. 31, p. 22, pl. 2, fig. 1-11.
1908 GIRTY, U.S.G.S. Prof. Paper 58, p. 153, pl. 31, fig. 17.
1915 MATHER, Bull. Sci. Lab. Denison Univ., v. 18, p. 132, pl. 6, figs. 8, 9.
1922 PLUMMER & MOORE, Texas Univ. Bull. 2132, p. 169, pl. 23, fig. 20-27.
1924 CORYELL in MORGAN, Okla. Geol. Survey Bull. 2, pl. 38, fig. 3-5.
1931 SAYRE, Kansas Univ. Sci. Bull. 17, p. 92, pl. 1, fig. 6-8.
1953 BASSLER in MOORE, ed., Treatise on Invert. Paleont., pt. G, Bryozoa, Geol. Soc. America and Kansas Press, p. *G*134, fig. 95, 4a-c.
1962 PERKINS, PERRY & HATTIN, Geol. Survey Kansas Bull. 157, pt. 5, p. 18-20, pl. 3, fig. 5-7.

Rhombopora lepidodendroides (?) MEEK

1899 KNIGHT, Jour. Geology, v. 7, p. 366.

Rhombipora lepidodendroides WHITE

1877 WHITE in WHEELER, U.S. Geol. Survey, v. 4, Paleont., p. 99, pl. 6, fig. 5a-d.

Rhombopora lepidodendroidea ULRICH

1884 ULRICH, Jour. Cincinnati Soc. Nat. History, v. 7, p. 27, pl. 1, fig. 1-1b.
1887 FOERSTE, Bull. Sci. Lab. Denison Univ., v. 2, pl. 7, fig. 3a, b.
1922 MORNINGSTAR, Geol. Survey Ohio, fourth ser., Bull. 25, p. 163-164.

Geinitzella ramosa var. ramosa multigemmata WAAGEN

1885 WAAGEN, India Geol. Survey, Paleont. Indica, ser. 13, pt. 1: 6, p. 883-884, pl. 112, fig. 2a-b; pl. 13, fig. 2a, b, 3, 4.

Geinitzella ramosa var. ramosa sparsigemmata WAAGEN

1885 WAAGEN, India Geol. Survey, Paleont. Indica, ser. 13, pt. 1:6, p. 883-884, pl. 12, fig. 1a, 1c, 4; pl. 13, fig. 1a-d.

MEEK's original locality was described as "Division C, of Nebraska City section, also in division B . . . ," also found at "Bennets Mill, Wyoming, Rock Bluff, and Plattsmouth" (MEEK, 1872, p. 141).

MEEK's specimens (now in the United States National Museum, Smithsonian Institution) were loaned to me for examination. Of the four (USNM 24532-1, -3, -5, -6), two (USNM 24532-1, -3) will be figured by HUFFMAN (in press; personal communication, 1970) as paralectotypes; the two others (USNM 24532-5, -6) will be unfigured paralectotypes. According to WASS (1969, p. 33-34), the type specimens were collected four feet above the Willard Shale in the Tarkio Limestone (Nemaha Subgroup, Wabaunsee Group, Upper Virgilian).

My measurements of MEEK's specimens are summarized in the tables of Appendix B as "Type Suite." Their locations in the dendrogram (Fig. 9) are indicated by: A001 for USNM 24532-5, A002 for USNM 24532-6, A003 for USNM 24532-3, and A004 for USNM 24532-1. The values obtained for all parameters, although larger than the mean of the Wreford Megacyclothem specimens, fall well within the total range of variability which I have recorded among the Wreford specimens. This is also obvious in the dendrogram.

The *Rhombipora* reference (WHITE, 1877) is perhaps a simple typographical error, as, on pages 26 and 99 *Rhombipora* appears (a total of four times) while on the page facing Plate VI, the explanation says that *Rhombopora* is figured. ULRICH's (1884) *lepidodendroidea* was presumably a deliberated action intended to "correct" the ending of *lepidodendroides* to agree with the ending of the genus. The *Geinitzella* reference is based on WAAGEN's figures (lithographs) and discussion. Those types are unknown (perhaps disappearing from the Berlin Museum in the interval 1939-1945), and DREYER (1961) says that the type locality is no longer available.

The total stratigraphic range known to me for *Rhombopora lepidodendroides* is Early Pennsylvanian to Late Permian. The oldest known specimens referred to *R. lepidodendroides* are Morrowan-Atokan, Pottsville (Ohio), cited by *Morningstar* (1922). PERKINS, PERRY, & HATTING (1962) in their excellent discussion, cite a transitional-age group of specimens from the Shawnee-Group, Virgilian (Kansas). This present citation for *R. lepidodendroides* is Wolfcampian, Council Grove-Chase (Nebraska, Kansas, Oklahoma). The youngest *R. lepidodendroides* referrence is that by GIRTY (1908) and is Guadelupian from the Capitan.

NEW SPECIES SYRINGOCLEMIS WREFORDENSIS

My non-*Rhombopora* Wreford rhabdomesid specimens are not the species which GIRTY described, although they can be referred to his genus *Syringoclemis*. Consequently, I propose here that they be considered a new species, *Syringoclemis wrefordensis*.

In the *Syringoclemis wrefordensis* specimens from the Wreford Megacyclothem, acanthopores are always numerous, never "scantily developed," and never of "two sizes," always of only one size in any zoarium, and there are never "areas . . . in which no acanthopores can be seen at all" (see my discussion of the skeletal morphology of *Syringoclemis wrefordensis,* and the tables of Appendix B). Furthermore, only four (out of 84) specimens of *Syringoclemis wrefordensis* had "six or less . . . zooecia . . . in 2 mm" (all quotes from GIRTY, 1911, p. 206-207).

GIRTY proposed the genus and species simultaneously (1911, p. 206-207), including "an epitheca" as part of the generic diagnosis for *Syringoclemis*. The arguments which I have advanced in my discussion of *Rhombopora* and *Rhabdomeson* apply equally well here. There was no other observable difference between specimens with basal laminae (epitheca) and without basal laminae. Plate 1, figures 13-15, show a gradational series like the one illustrated for *Rhombopora lepidodendroides*.

I therefore propose that the genus *Syringoclemis* be emended to include both these growth variants observed in the Wreford Megacyclothem. One growth form is a solid, cylindrical, ramose form; the other growth form is identical to the first except for the presence of a basal lamina.

As in *Syringoclemis biserialis, S. wrefordensis* has no

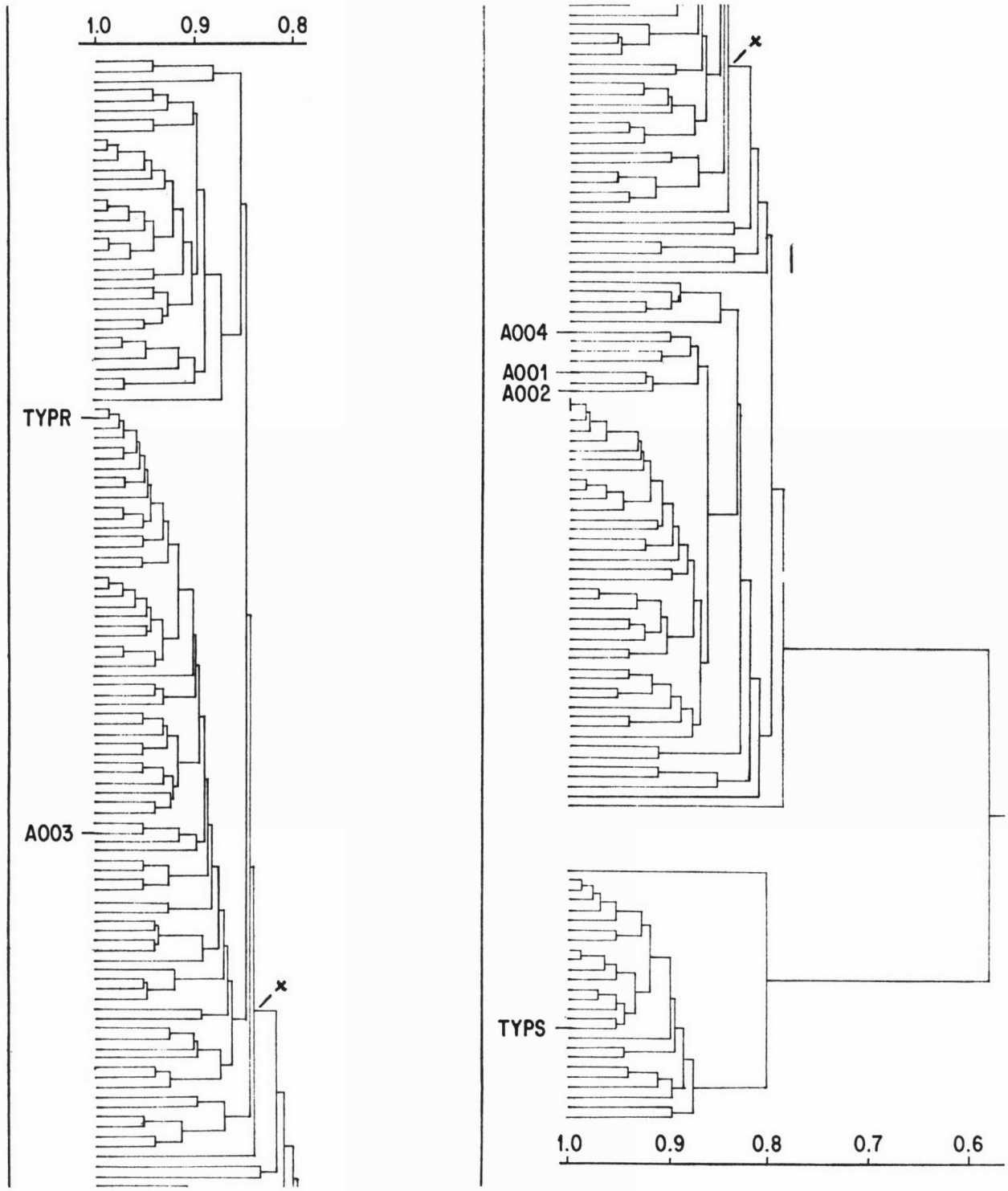


FIG. 9. Dendrogram of Wreford Rhabdomesidae. Figures at top and bottom denote similarity coefficients. Common point of left and right parts of figure marked by "X."

diaphragms in either zooecial tubes or mesopores. The mesopores of both are confined to the peripheral zone. The mesopores are arranged similarly in both and are roughly of the same size (0.09 to 0.10 mm for *S. biserialis,* 0.04 to 0.13 mm for *S. wrefordensis*).

Complete examination of this species is undertaken in the skeletal morphology section and numerical observations are summarized in the tables of Appendix B. Plate 1, figures 7-9, and 13-15, are illustrations of all type material.

The following are designated as types for the new species and they are located in the collections of the Paleobryozoological Research group of The Pennsylvania State University Department of Geology and Geophysics: CY15(4) (float)-p-PC-6101, the holotype (one-half zoarium in epoxy, plus three peel-sections); WA08Be (u ½)-bfN-PC-6101, paratype (one-half zoarium in epoxy, plus three peel-sections); PT15C(u ⅛)-bfN-PC-6101, paratype (one-half zoarium in epoxy plus three peel-sections). The holotype (CY15(4)) is of the solid-ramose type; paratype PT15C has an axial basal lamina and encrusts a brachiopod spine; paratype WA08Be is a supplemental specimen showing TP, MMSP, NMA and NMSP nicely.

SKELETAL MORPHOLOGY OF WREFORD RHABDOMESIDAE

SKELETAL MORPHOLOGY OF RHOMBOPORA LEPIDODENDROIDES

GENERAL ORIENTATION OF COLONY

Some initial clarification of some of the terminology used herein is necessary. This short discussion applies also to *Syringoclemis* (indeed, to all ramose cryptostomes). Bryozoologists have long been burdened by an awkward and redundant terminology. Laudably, Bassler (1953) made one of the few attempts to discard synonymous terms from our nomenclature. On the other hand, Ryland (1968) created several new terms for etymological reasons, thus bringing the total glossary of bryozoan terminology up to about 2,000 entries. All of the terms advanced by Ryland are synonymous with earlier descriptive words; as nothing seems to be gained by coining redundant descriptive nomenclature, only the most widely used of the existing terms are employed by me here.

Ramose bryozoans grow away from an ancestrula or founder zooid. Ramose cryptostomes accomplish this growth by adding new zooecia at the growing tip of a branch. The direction from ancestrula to growing tip is defined as **distal**; the opposite direction is **proximal.** The zooecium (plural, zooecia) is the tube in which the individual zooid (polyp) lived. The zooecium in the Rhabdomesidae is a cone with a flexure near the outside of the zoarium (plural, zoaria, the entire colony). This tapering tube has the tip of its cone at the center of the colony and its widest dimension at the aperture (external opening). The direction from the tip at the axis of the colony to the external aperture is defined as **abaxial. Adaxial,** of course, is the opposite direction. Thus, the statement, "hemisepta occur on the distal zooecial wall adaxially to the first diaphragm" has only one meaning, is concise, and needs no special interpretation.

Table 7 summarizes the numerical morphological characters of the Wreford *Rhombopora lepidodendroides.* It is given here so that this species can be readily compared with other bryozoans described in similar fashion. More information of this type is also given in Appendix B.

Table 7. *Summary of Measurements Made on Wreford Specimens of* Rhombopora lepidodendroides Meek, *1872.*

Character	Mean	Standard Deviation	Range	Coefficient of Variation	Numbers of Measurements*
MWZ	1.67	0.67	0.5 - 4.4	40.3	579
TP	0.385	0.186	0.06- 1.40	48.4	567
Z1	9.4	1.9	5-19	20.4	533
Z2	5.3	1.0	4-9	19.4	527
ZA	14.0	4.0	7-33	28.4	558
MZAD	0.260	0.044	0.14- 0.53	16.7	578
AZD	0.996	0.366	0.40- 3.10	36.8	524
IWT	0.123	0.041	0.03- 0.31	33.4	563
NMSP	0.6	1.4	0-16	244.8	540
MMSP	0.088	0.030	0.03- 0.21	33.9	133
NMA	11.7	3.1	1-22	26.3	526
MMAW	0.085	0.023	0.03- 0.17	27.5	564
NRIW	2.1	0.7	1-4	35.8	531
NMU	41.3	11.5	11-72	27.8	524
MNUW	4.1	1.0	1-7	24.6	528
MMUW	0.045	0.011	0.02- 0.08	23.8	574
DTZ_2	1.9	2.7	0-15	141.9	543
NSHS	0.0	0.0	0-0	0.0	543
NIHS	0.0	0.0	0-0	0.0	543
BSL	.....	.....	0.01- 0.02	.....	48

* 1 measurement per specimen.

WALL STRUCTURE

Throughout this discussion, "wall" refers to the calcified zooecial tubes built by the zooids of the colony. In the Ectoprocta, there are two distinct portions of zooecial walls. Tavener-Smith (1969), Boardman (1960), Boardman & Cheetham (1968), and Elias & Condra (1957) have presented excellent discussions about these two for other bryozoan groups. In the Rhabdomesidae, the two portions, slightly modified from Tavener-Smith's (1969) terminology for the fenestrate cryptostomes, are an inner, primary skeletal wall (comprising the central

part of colony branches, analogous to the axial region of the trepostomes) and an outer, laminated skeletal wall (comprising the outer rind of colony branches, analogous to the peripheral region of trepostomes).

The inner, primary, nonlaminated wall is seen, under magnification in thin sections, to be made up of a few (three to ten) fibers parallel to the central axis of the zooecial tube. These fibers are actually tiny, elongate crystals of calcite and are formed by the zooidal epithelium (see my more extended discussion under "Soft-part Morphology of the Rhabdomesidae"). Abaxially, these fibers blend with the outer, laminated wall layers.

The junction between the inner and the outer wall marks the position of the orifice. From the orifice, abaxially, to the aperture at the zooecial surface, is the region of the zooecial tube called the vestibule. The presence of this vestibule is one of the distinguishing criteria of the Cryptostomata. My measurement TP (thickness of the peripheral zone) is taken from the point of juncture of the inner, nonlaminated wall with the outer, laminar wall and is a measure of the thickness of the vestibular region.

The outer, laminated skeletal wall is composed of a series of mosaic sheets of calcite plates. TAVENER-SMITH (1969), based on WILLIAMS' (1968) study of brachiopod shell structure, suggested that these layers represent growth laminae of diurnal periodicity. *Hornera*, a living cyclostome bryozoan, was examined (BORG, 1926; TAVENER-SMITH, 1969) in this light. The number of growth laminae closely approximated the age in days of this modern genus. A few counts of laminae were made by me on Wreford rhabdomesids. The age of a typical robust (2.2 to 2.8 mm MWZ) *Rhombopora lepidodendroides*, based on these counts, was inferred to have been 325 to 380 days. The extreme difficulty in making these counts prevents any reliable estimates of age based on statistically rigorous data. It seems reasonable to suggest, however, that at death the largest of the *R. lepidodendroides* colonies (MWZ greater than 2.9 mm) were about a year and a half to two years old.

Figures 10 and 11 illustrate the various relationships discussed here. The soft parts in the figures will be explained subsequently, as mentioned above.

ACANTHOPORES

Acanthopores are spinose projections on the external surfaces of bryozoan zoaria. They can be recognized in tangential sections as concentrically laminated structures situated in the interapertural space. In longitudinal and transverse sections, they are seen to be a series of nested cones composed of adaxially concave laminae. Acanthopores are confined to the peripheral zone (the zone of outer, laminated skeletal walls). Two types are found in *Rhombopora lepidodendroides,* megacanthopores and micracanthopores.

Acanthopores are commonly described as being lumens surrounded by a centrally perforate cone-in-cone structure (see, for example, BASSLER, 1953, p. *G7*, or PERKINS, PERRY, & HATTIN, 1962, p. 19). Under the greater magnifications used by me (up to 250 diameters), this central lumen can be seen to be crossed by laminae of the surrounding outer, laminated skeletal wall. The laminae do not cross normal to the axis of the acanthopores but are domed abaxially. As a consequence of this doming, the laminae are spread farther apart than they normally are in the peripheral zone, giving the illusion (under lower magnifications) of a central lumen. The space between these separated laminae is occupied by a clear, sparry calcite which extends infinitesimally into the enclosing peripheral laminae. In the fenestrate cryptostomes, skeletal rods are composed of this same sparry calcite. TAVENER-SMITH (1969) suggests that these same sparry skeletal rods of the fenestrates are simply structural support elements lending cohesion and rigidity to the wall fabric. If the acanthopores of the rhabdomesid cryptostomes are analogous to the skeletal rods of the fenestrate cryptostomes, then the acanthopores of the trepostome

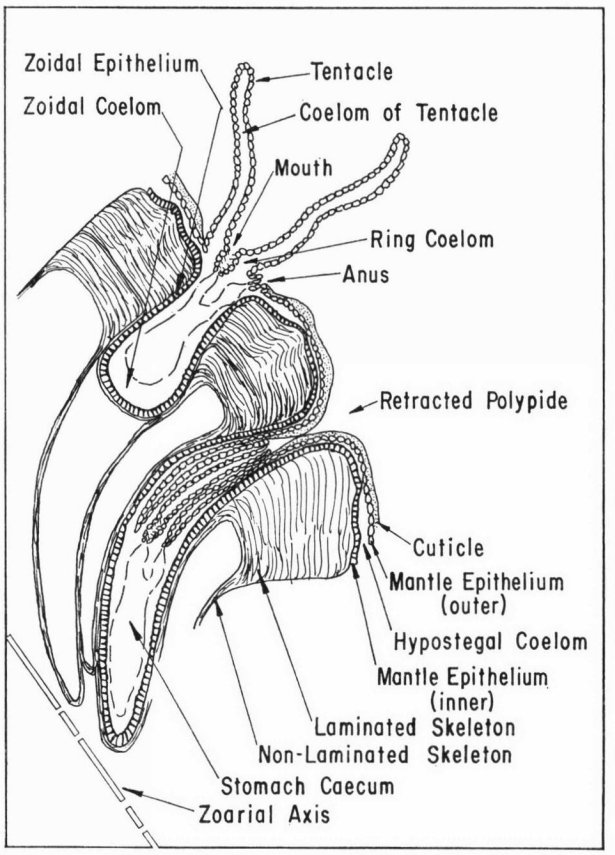


FIG. 10. Reconstruction of the mature rhabdomesid zooid in its extended state (upper zooid) and retracted state (lower zooid) with their relationships to the zooecial wall regions.

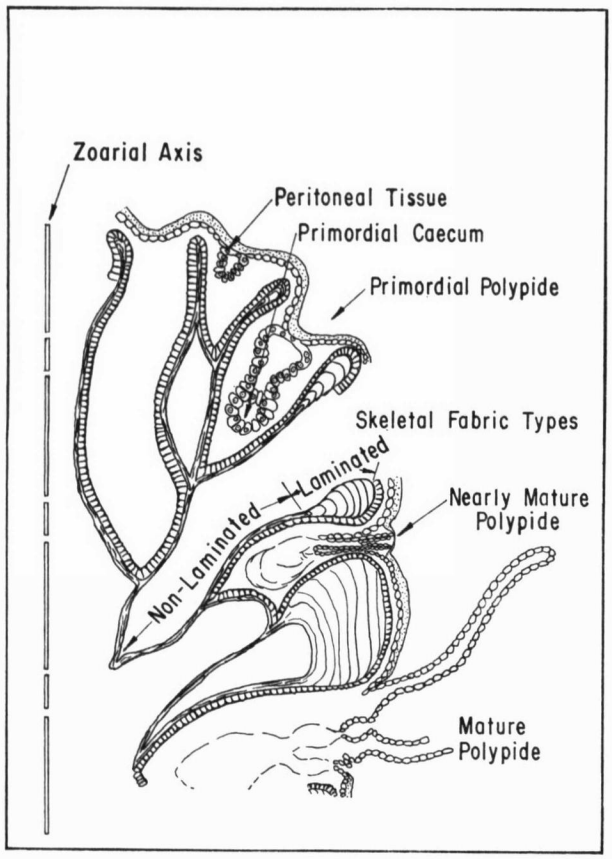


FIG. 11. Reconstruction of a typical growing tip of a rhabdomesid cryptostome showing soft-part relationships to zooecial wall regions.

bryozoa, which *are* axially lumenate, are neither analogous nor homologous.

The commonly accepted theory is that cryptostomes, trepostomes, and cyclostomes evolved from ctenostomes or ctenostome-like bryozoans. The ctenostomes do not possess now, nor can they be shown to have ever possessed, acanthopore-like structures. If the ctenostome bryozoans are the ancestral stem of the bryozoans, then these two similar-appearing structures (trepostome acanthopores and cryptostome acanthopores) should not be regarded as homologous unless the ancestor can be shown to have possessed a part (organ? polyp? zooid?) with the same structure or function.

Megacanthopores are located within the interapertural space and do not project into the zooecial apertures of *Rhombopora lepidodendroides* MEEK. At their greatest diameter, they are generally greater than 0.05 and less than 0.10 mm. They project, when observable in very well preserved zooaria, a maximum of 0.20 mm above the zooarial surface. Generally, one megacanthopore is located at the distal extremity of each zooecial aperture, and another at the proximal extremity. Others are found scattered randomly in the interapertural space over the colony surface.

Between the megacanthopores, and arranged in one to four parallel rows, are the smaller and more numerous micracanthopores. In some specimens (see Pl. 2, fig. 2-4), there is no size difference between megacanthopores and micracanthopores; in some other specimens, there is only a slight difference in acanthopore sizes. Generally, however, micracanthopores and megacanthopores are of two distinctly different sizes. The continuously intergradational nature of the megacanthopores and micracanthopores has already been noted in the systematic analysis of the Wreford Rhabdomesidae. The smaller micracanthopores (those 0.03 mm and less in diameter) are simple, circular-in-tangential-section, domal protuberances, which project .001 mm and less above the colony's surface, and are composed of dark granules.

Acanthopores proved to be enormously important in interpreting the physiology of *Rhombopora lepidodendroides,* as discussed later under soft part morphology of the Rhabdomesidae.

HEMISEPTA

Hemisepta are minute, shelflike projections into the zooecial tube from the zooecial walls. The presence of hemisepta is usually regarded as one of the chief distinguishing characteristics of the cryptostome bryozoans (BOARDMAN & CHEETHAM, 1969). Commonly, hemisepta occur at the base of the vestibule, and for this reason hemisepta are considered to have performed as a support and pivot point for an hypothesized opercular structure. Hemisepta are of two types, inferior and superior.

However, this feature—even though central to the concept Cryptostomata—is confusingly, contradictorily, and ambiguously defined in the literature. SHROCK & TWENHOFEL (1953), based on ULRICH (1895), define the inferior hemiseptum as that hemiseptum which projects from the proximal wall; that is, it arises from the inferior (proximal) wall. BASSLER (1953), in the currently definitive work, defines the inferior hemiseptum as the hemiseptum projecting from the distal wall. That is, it projects downward, in an inferior (proximal) direction. In their text, MOORE, LALICKER, & FISCHER (1952) refer to all hemisepta by the single term "hemiseptum," regardless of from which wall a hemiseptum projects.

Here, I will follow the usage of BASSLER (1953). That is, superior hemisepta project from the proximal side of the zooecial tubes, inferior hemisepta arise from the distal side.

In the 1,027 rhabdomesid specimens from the Wreford Megacyclothem, only sixteen possible hemisepta were observed. None of these hemisepta is unequivocally an hemiseptum. Neither MEEK's (1872) original description nor all the subsequent work on *Rhombopora lepidodendroides* mentions hemisepta. It seems, therefore, that *Rhombopora lepidodendroides* has no hemisepta. The

few hemiseptum-like projections observed by me (Pl. 2, fig. 15) in the Wreford Megacyclothem population are apparently local aberrations of the zooecial wall, rather than true hemisepta. Two lines of reasoning support this conclusion. The first is that these projections do not occur in every zooecium of the zooaria in which they are known. Hemisepta of other species occur in approximately the same position and number in all zooecia belonging to those species. The second point is that these hemisepta-like wall elements do not occur at the base of the vestibule. Although there are a few exceptions, the rule in cryptostomes is that one hemiseptum will be at the orifical limit of the vestibular tube.

DIAPHRAGMS

Diaphragms are transverse partitions within the zooecial tube. They occur throughout the zooecial tubes, and generally the plane of the diaphragm is at right angles to the long axis of the zooecium. Diaphragms occur in 48% of the Wreford specimens of *Rhombopora lepidodendroides*.

Diaphragms are continuous with the outer, laminated skeletal wall. Forming the diaphragm, the laminae of the peripheral zone can be seen (Pl. 2, fig. 7; Fig. 10) to loop adaxially into the zooecial tube and then to loop back abaxially into the peripheral zone on the outer side of the zooecium. Since the diaphragms of *Rhombopora lepidodendroides* in the Wreford are composed of three to five laminae, it may be suggested that diaphragms are deposited rather rapidly. In fact, following previous suggestions that the laminae of the peripheral zone represent diurnal periodicity, three to five laminae would indicate three to five days.

Diaphragms of the Rhabdomesidae are complete. This means that there is no communication between one side of the diaphragm and the other. In many Bryozoa, particularly trepostomes (see, for example, CUFFEY, 1967), there are several diaphragm types present in a single specimen. They may be perforate, imperforate, curved, planar, septate, or incomplete. Another set of terms describes other variations (such as heterophragms, cystiphragms and hemiphragms) in diaphragm morphology. No departures from planar, imperforate diaphragms were observed in the Wreford specimens.

Because the laminated outer skeletal walls are deposited over the colony as a whole by the mantle epithelium and because the laying-down of this imperforate barrier necessarily seals off the adaxial portion of the zooecial tube, diaphragms must represent growth interruptions, either caused by the death of the individual zooids or by reduction (or degeneration) of the zooids. Perhaps this reduction was concerned with reproduction. However, nothing is known about reproduction in the cryptostome bryozoans. Modern calcified cyclostome and cheilostome bryozoans produce special reproductive structures called ovicells or ooecia or gonozooecia, which serve as larval brood chambers. No structures other than normal zooecial tubes are known in *Rhombopora lepidodendroides*.

Cryptostome bryozoans, when compared with trepostome, are very simply constructed, and simple explanations are often best for the various observed structures. Following this idea, it may be that diaphragms are nothing more than simple support structures. Two things may well have happened at about the same time. First, the zooid's size reached some physiological limit, and second, the zoarial radius reached some sort of structural limit. These two things combine, causing the zooids to secrete a platform (the diaphragm), which helped solve both problems. Diaphragms solve the first by reducing the volume of the zooecial tube so that the zooid is more congruent with its surroundings, and the second by enabling radial increase through stiffening the fabric of the zooarium. In D'ARCY THOMPSON's (1966) experiments, an unsupported cylinder reached its structural limit when the length is roughly three times its diameter. His discussion devoted to blood vessels (THOMPSON, 1966, p. 125-131) illustrates my point as well. Blood vessels cannot simply increase in radius. They, as the ramose rhabdomesid cryptostome cylinders, must strengthen their whole fabric. This is done chiefly by the vessels building much thicker walls of much stronger material. *Rhombopora lepidodendroides* had no selection of building materials so that, when enlarging its radius, it maintained structural rigidity by secreting diaphragms. The basal laminae occasionally found in Wreford rhabdomesid colonies may possibly also have served this same function.

BASAL LAMINAE

The basal lamina is also known as an epitheca. Synonyms also in use are coenelasma and epizoarium. Since workers on the cheilostome bryozoans use the term epitheca to denote the outer and frontal membranes and the ectocyst, all three of which are chitinous rather than calcareous, I suggest that the term basal lamina be restricted to the usage discussed here.

Basal laminae are secreted by the zooids' epithelium upon surfaces such as brachiopod spines, pelecypod shells, rock faces, seaweeds, and algal fronds. From this lamina arise the zooecial tubes. Basal laminae in *Rhombopora lepidodendroides* (as well as in *Syringoclemis wreforden-sis*) are made up of three to six laminae of primary wall material.

Basal laminae are known to occur in two ways in *Rhombopora lepidodendroides*. The first is the encrusting type; the second is the axial tube type.

The encrusting type of basal lamina consists of a basal plate (the lamina) from which arises a single layer of zooecial tubes. Several forms of this encrusting type are illustrated in the plates. Two forms are most common. These are encrustations upon brachiopod shells or their surfaces and encrustations upon *Rhombopora lepidodendroides* or other bryozoans. In Plate 2, figure 1, I have

shown a *R. lepidodendroides* of the encrusting type overgrowing a ramose *R. lepidodendroides*. As mentioned above in the diaphragm discussion, this basal lamina may function as a structural strengthening device. The presence of a greatly thickened peripheral zone certainly would create great strength. Because in many specimens (Pl. 2, fig. 1), the basal laminae warp down into the zooecial tubes which they are overgrowing to form diaphragms, I suggest that in some specimens overgrowth may be accomplished by the colonial epithelium, rather than by the expansion of newly-formed colonies establishing themselves on a suitable substrate (here, a previously existing *R. lepidodendroides* colony). That is, autoovergrowth has taken place.

The second type, the axial tube type of basal lamina, is really not a separate form, but is the form taken by a lamina when encrusting a narrow cylindrical object. However, because of the problems of a taxonomic nature discussed in the systematics portion of this paper—namely the concept *Rhabdomeson* versus the concepts *Rhombopora* and *Syringoclemis*—I have erected this separate category for the axial tube type of basal lamina. These are basal laminae which were deposited by the bryozoan upon cylindrical surfaces. When this surface was an echinoid spine or brachiopod spine, the spine is commonly preserved as well (Pl. 1, fig. 10). When this cylindrical surface was of less permanence, such as an algal frond, only the encrusting, cylindrical lamina with its outbranching zooecial tubes is preserved. The taxonomic implications of these observations have previously been discussed.

MESOPORES

Mesopores are small, zooecium-like tubes scattered throughout the colony. Here, as with the acanthopores, there seems again to be a structure of cryptostome bryozoans bearing the same name as a trepostome structure, but with the two being possibly quite different. In Plate 1, figure 10, I have illustrated a mesopore from *Batostoma?* (Liberty Formation, upper Richmond, Ordovician, Madison, Indiana), a trematoporid trepostome. The mesopores of trepostomes are characterized by having more diaphragms in them than do the adjoining zooecial tubes.

The mesopores of *Rhombopora lepidodendroides* have no diaphragms in them. Another difference between trepostome mesopores and those observed in *R. lepidodendroides* is that typical trepostome mesopores extend adaxially well into the colonial axis. On the other hand, mesopores (like megacanthopores and micracanthopores) in the Wreford rhabdomesids—and, based on cursory examination of representatives from twenty other rhabdomesid genera, all rhabdomesid genera—do not extend adaxially more than the thickness of the peripheral zone which encloses them. The mesopores of *R. lepidodendroides* are only slight in-warpings of the outer, laminated skeletal wall. It is not clear what function they might have fulfilled. Commonly the mesopores of trepostomes are interpreted as being the dwelling tubes of accessory zooids or kenozooids, serving the colony much as vibracular and avicularial kenozooecia serve the cheilostome bryozoans. In *R. lepidodendroides,* however, the mesopore is floored by outer, laminated skeletal wall, thus implying that the mesopore was not secreted by a zooidal epithelium but by the outer colonial mantle epithelium. Since the zooid-containing portion of all zooecial tubes is walled by material apparently deposited by zooidal epithelium, I suggest that these rhabdomesid mesopores, therefore, represent something other than kenozooecia. In keeping with my earlier suggestion that simpler explanations seem to yield more reasonable interpretations for cryptostome bryozoans, I propose that the mesopores of *R. lepidodendroides* represent nothing more complicated than simple infoldings of the zoarial surface, perhaps as an attempt to achieve greater structural rigidity, perhaps for no particular functional purpose at all. Mayr (1963, p. 158-163, 168-172) discusses the general concept of genes which, while producing one phenotypic change directly, affect other phenotypic characters indirectly. Often, therefore, nonfunctional elements are maintained in populations by selection for functional ones. This type of explanation could possibly account for the presence of nonfunctional mesopores in *R. lepidodendroides.*

MISSING SKELETAL ELEMENTS

A number of structural features were not observed in any specimen of *Rhombopora lepidodendroides* from the Wreford Megacyclothem. These include monilae or other beading of the zooecial walls, maculae or monticules or any other such irregularity in the number or size of arrangement of zooecia, stoloniferous or other proplike supporting elements, kenozooecia of any type, and brown bodies.

SKELETAL MORPHOLOGY OF SYRINGOCLEMIS WREFORDENSIS

GENERAL COMMENTS

My remarks in this section are largely limited to morphological elements which are unique to *Syringoclemis wrefordensis.* Obviously, proximal, distal, and other such terms of orientational nomenclature will be identical to those used for *Rhombopora lepidodendroides,* and a duplicate discussion of them will not be offered here. As *R. lepidodendroides* and *S. wrefordensis* are in the same family and therefore share many characters in common, there is a high degree of correspondence in the structure and distribution of morphologic elements. Again, a summary of the numerical morphological characters of *S. wrefordensis* is presented here (see Table 8; see also Appendix B).

WALL STRUCTURE

The calcified walls of the zooecial tubes in *Syringo-*

clemis wrefordensis are divisible into inner, nonlaminated and outer, laminated portions, just as in *Rhombopora lepidodendroides*. Also, being a cryptostome, this new species possesses an orifice, vestibule, and aperture at the abaxial end of each zooecial tube. However, the peripheral zone is much less pronounced in *S. wrefordensis* than it is in *R. lepidodendroides* (see the tables of Appendix B and Plates 1 and 2 for comparisons). Counting the number of laminae in the peripheral zone was much more difficult in *S. wrefordensis* than in *R. lepidodendroides* because the laminae are so much closer together.

TABLE 8. *Summary of Measurements Made on Wreford Specimens of* Syringoclemis wrefordensis *Newton, n. sp.*

CHARACTER	MEAN	STANDARD DEVIATION	RANGE	COEFFICIENT OF VARIATION	NUMBER OF MEASUREMENTS*
MWZ	1.10	0.30	0.5 -1.8	27.1	77
TP	0.170	0.062	0.09-0.31	36.3	77
ZI	14.0	7.1	7-32	50.5	79
Z2	9.0	2.0	5-15	22.2	77
ZA	16.6	4.3	10-23	25.8	76
MZAD	0.180	0.029	0.14-0.30	16.2	76
AZD	0.643	0.223	0.30-1.90	34.6	77
IWT	0.030	0.008	0.02-0.11	27.2	76
NMSP	37.1	13.7	8-67	36.9	77
MMSP	0.074	0.024	0.04-0.11	32.5	76
NMA	37.3	14.2	17-111	38.1	77
MMAW	0.035	0.010	0.02-0.06	28.6	77
NRIW	0.0	0.0	0-0	0.0	79
NMU	0.0	0.0	0-0	0.0	79
MNUW	0.0	0.0	0-0	0.0	79
MMUW	(Not applicable because micracanthopores are absent)				
DTZ_2	0.4	1.1	0-7	282.8	76
NSHS	0.0	0.0	0-0	0.0	76
NIHS	0.0	0.0	0-0	0.0	76
BSL	....	....	0.01-0.02	.....	30

* 1 measurement per specimen.

For specimens with a TP of 0.18 mm and an MWZ of 1.20 mm, the average number (based on only five counts) of laminae was about 200. For *R. lepidodendroides* MEEK with a TP of 0.18 mm, only about 120 laminae were counted (average based on four observations). This indicates that radial expansion was only about one-half as rapid in *Syringoclemis* as it was in *Rhombopora*. However, since I collected only 84 specimens of *Syringoclemis* from the Wreford Megacyclothem and, since 38 of those came from only two localities which are both in the upper Speiser calcareous shale, I do not feel it well advised to generalize my conclusions based on these data. One suggestion that it is perhaps safe to make is that *S. wrefordensis,* relative to *R. lepidodendroides,* was less robust; that is, *Syringoclemis* would have been more susceptible to the rigors of its environment than was *Rhombopora*. This relative delicacy of size and slow growth rate may have been the principal contributing factors to its eventually having been competitively excluded by *R. lepidodendroides*.

ACANTHOPORES

One of the primary differences between *Rhombopora lepidodendroides* and *Syringoclemis wrefordensis* lies in the acanthopores. For purposes of comparison, I refer to the acanthopores of *Syringoclemis* as megacanthopores, but, in any given zoarium of *Syringoclemis,* only one size of acanthopore is present; no distinction can be made here between megacanthopores and micracanthopores.

As in *Rhombopora lepidodendroides,* acanthopores are confined to the peripheral region in *Syringoclemis wrefordensis*. They project less than 0.04 mm above the zoarial surface and only 0.02 to 0.025 mm adaxially into the peripheral zone. This means that extremely shallow tangential sections are required to study the acanthopores of *S. wrefordensis*. As mentioned above, growth laminae are much closer together; this results in the domed laminae of the *Syringoclemis* acanthopore being concomitantly closer together. Neither a central lumen nor a core of clear, sparry calcite was observed in these acanthopores. This probably is attributable to the close-set nature of the acanthopore laminae. Another difference lies in the abundance of the acanthopores; in *R. lepidodendroides,* NMA averages about 12, while in *S. wrefordensis,* NMA averages about 37. The acanthopores of *S. wrefordensis* deflect inward the boundaries of both zooecial apertures and mesopores, a situation never observed in *R. lepidodendroides*. The megacanthopores of *R. lepidodendroides* (as discussed above) are usually found at the distal and proximal end of each zooecial aperture, with linear rows of micracanthopores in between them. No consistent pattern of distribution was observed for the acanthopores of *S. wrefordensis*; a scattered ubiquity was the rule. The number of acanthopores per square millimeter in *R. lepidodendroides* (sum total of the NMA mode plus the NUM mode) is 48. The number of acanthopores per square millimeter (the NMA mode) in *S. wrefordensis* is 42. That is, the total number of spinose projections per unit area is roughly the same in the two Wreford rhabdomesids. This point will be referred to later in my discussion on soft parts.

HEMISEPTA

No hemisepta or hemiseptum-like projections were observed in any zooecium of any zoarium of *Syringoclemis wrefordensis* in my samples from the Wreford Megacyclothem. As the shelf-like aberrations of the zooecial wall in *Rhombopora lepidodendroides* were judged not to be hemisepta, I conclude that neither Wreford rhabdomesid possessed these structures.

DIAPHRAGMS

All of the diaphragms of *Syringoclemis wrefordensis*

in the Wreford Megacyclothem are complete and lie at right angles to the zooecial axis. The diaphragms of *S. wrefordensis* are in all respects similar to those of *Rhombopora lepidodendroides* MEEK.

Diaphragms occurred in 16% of the specimens observed, a figure which is one-third that obtained for *Rhombopora lepidodendroides*. Perhaps the smaller size of *Syringoclemis* precluded any need for their general development (see my discussion of diaphragms under skeletal morphology of *Rhombopora lepidodendroides*). Possibly the fact that the laminae of *Syringoclemis'* peripheral zone are closer together than those of *Rhombopora* indicates greater structural rigidity in *Syringoclemis*; hence, a structural "need" for diaphragms may not have existed.

BASAL LAMINAE

Basal laminae occur in 40% of all Wreford Megacyclothem *Syringoclemis wrefordensis* colonies, a figure many times the 1% occurrence observed for *Rhombopora lepidodendroides*. This indicates, bearing in mind the limited size of the *S. wrefordensis* sample, that this species had a strong preference for an encrusting habit. Considering this species' relatively slower growth rate, this might have constituted a limited selective advantage. Note that *Syringoclemis'* general robustness was less than that of *Rhombopora*. However, *Syringoclemis'* encrusting habit may have compensated for this. Its smaller MWZ values indicate that *S. wrefordensis* would have been limited in its overall height (THOMPSON, 1966, and discussed elsewhere herein for *R. lepidodendroides*): therefore, in soft muddy bottoms, these colonies' small size, coupled with their slow growth rate, would have been powerfully disadvantageous. However, being encrusted on a brachiopod spine, echinoid spine, or algal frond would have kept *S. wrefordensis* colonies well above the potentially smothering bottom environment; *R. lepidodendroides* achieved this instead by simply growing larger or more robust colonies. Thus, the encrusting form was more selectively advantageous for *Syringoclemis* than for *Rhombopora*. GIRTY's (1911) definition of the genus (discussed in the systematics portion of this paper) included only forms with a cylindrical basal laminae. It is probable then, that the potential for the development of a basal lamina was an important genetic attribute throughout the known stratigraphic range of the genus.

MESOPORES

The mesopores of *Syringoclemis wrefordensis* are considerably different from those of *Rhombopora lepidodendroides*. As in *R. lepidodendroides,* they are without partitions (tabulae, diaphragms). The mesopores in *S. wrefordensis* are considerably more abundant (NMSP averaging about 37) than in *R. lepidodendroides* (NMSP averaging less than 1). Also, the mesopores of *Syringoclemis* are apparently much more than simple infoldings of the surface. Some mesopores of *Syringoclemis* extend adaxially below the peripheral zone, particularly in specimens with basal laminae (though this condition is not restricted to such specimens). Their greater depths suggest that the *Syringoclemis* mesopore may have served some important function in the colony.

Perhaps each mesopore contained a kenozooid. However, if this were the case, it is difficult to understand what advantage there would have been in having as many as 40 or so accessory zooids per square millimeter of zoarial surface. But, if these kenozooecia served to create feeding currents or to keep the zooecial apertures free from debris, then a clear advantage is evident. The enhanced feeding ability would have been beneficial to either the encrusting forms above the bottom or to the ramose forms upon the bottom. As kenozooecia serving to prevent the closing-off of zooecia, they would be more advantageous to the ramose colonies on the bottom than to the encrusting forms on spines or algal fronds. Since mesopores are floored and walled with outer, laminated skeletal wall material, it is not clear just what sort of kenozooid might have been involved (see the discussion of soft parts), if mesopores served this function.

As an alternative to feeding-enhancing or debris-sweeping, mesopores may conceivably have functioned in reproduction. Each mesopore chamber could possibly have nurtured one to several larvae up to the free-swimming state, and then released them. Each mesopore might have been lined with inner mantle epithelium, filled with a modified hypostegal coelom, and covered over by the outer mantle epithelium and the cuticle. Fertilization could then have occurred in the zooidal coelom with the zygotes migrating into the mesopores through the contiguous hypostegal coelom. This is not an entirely hypothetical suggestion; HYMAN (1959, p. 344-347) suggests that autogamous fertilization may be the rule in Ectoprocta, although very little experimental evidence seems to be available.

MISSING SKELETAL ELEMENTS

The skeletal elements missing in *Rhombopora lepidodendroides* are also absent in *Syringoclemis wrefordensis,* except that kenozooecia might possibly be present in *Syringoclemis*. Also, *S. wrefordensis* lacks micracanthopores, which are a prominent feature in *R. lepidodendroides*.

SOFT-PART MORPHOLOGY OF THE WREFORD RHABDOMESIDAE

No direct observation of rhabdomesid cryptostome soft parts is possible, of course. Nonetheless, much interest in such materials has recently been generated among paleobryozoologists, and research into this area is going on apace (BOARDMAN, personal communication, 1969). Recent articles of particular note are those by BOARDMAN

& CHEETHAM (1969, especially fig. 1 and 2) and by TAVENER-SMITH (1969, fig. 2, 5-6, 8).

Reference to Figures 10 and 11 throughout this discussion will be of help in visualizing the relationships between soft parts and skeletal hard parts. This discussion is based almost entirely on sections of *Rhombopora lepidodendroides,* but these remarks apply equally well to *Syringoclemis wrefordensis.*

The close relationship of bryozoans to brachiopods suggested to TAVENER-SMITH (1969) the possibility of using WILLIAMS' (1968) work on brachiopod shell structure as a key to the understanding of fenestellid cryptostome wall structure. My interpretation of the soft-part relationships of the Wreford Rhabdomesidae is based on an extension of TAVENER-SMITH's excellent observations. Figure 11 is a representation of the growing tip of specimen GE01Da (float)-p-PC-4024, which is also illustrated photographically (Pl. 2, fig. 13). It was this section that led me to the interpretation expressed herein.

Since this splendidly preserved growing tip is the point at which the bryozoan's soft-parts created new skeletal material, I tried to fit the BORG (1926, fig. 55) zooid into the zooecial tubes of *Rhombopora lepidodendroides.* The BORG zooid fit readily enough, but the work of BOARDMAN & CHEETHAM (1969) and TAVENER-SMITH (1969) suggested a more complete picture to me. Assuming that the Wreford rhabdomesids were eucoelomate, as are the living ectoprocts, and assuming the TAVENER-SMITH model of zooidal epithelium and zooidal coelom surrounding the gut of the zooid, I assembled the uppermost zooid shown in Figure 10.

It is important to note that once the inner skeletal wall was established in the rhabdomesid cryptostomes, it was never added to; only the outer, laminated wall (the peripheral zone) increased in thickness. The inner mantle epithelium laid down the laminated skeletal fabric of the peripheral zone continuously (on an apparently diurnal basis) throughout the life of the colony.

The zooidal epithelium, which lined the zooecial tube, was not further involved in the formation of new skeletal wall, except during the development of diaphragms across the zooecial tubes. At that time, there occurred an episode of a few days' duration (see the discussion of diaphragms in the skeletal morphology section) during which, in concert, the inner mantle epithelium and the zooidal epithelium laid down a set of laminae. These laminae in the peripheral zone are indistinguishable from the other laminae of the peripheral zone, except that they are continuous with the laminae comprising the diaphragm. The conclusion, therefore, is that the zooidal epithelium laid down the laminae of the diaphragm simultaneously with the inner mantle epithelium laying down the extension of the diaphragm laminae into the interapertural portion of the peripheral zone.

If it is also assumed that the rhabdomesid zooid was retractile (as in most modern bryozoans), an interpretation of other structures can also be made. The lower zooid of Figure 10 is shown in the retracted condition. Several concomitant changes have occurred in the external distribution of soft parts, as compared to the arrangement in the extended zooid. Before examining these, however, a brief discussion of the basic body organization is necessary. Reference to Figure 10 will aid in visualizing the arrangement of tissues. This discussion is a précis of TAVENER-SMITH (1969).

Everywhere externally, the colony was covered by a cuticle. This cuticle served as protection against both the osmotic effects of the ambient sea water and modest predation (such as that due to small gastropods, small arthropods, or marine worms). Inside the cuticle was the outer mantle epithelium which secreted the cuticle. The use of "mantle" in this conjunction is based on TAVENER-SMITH's (1969, p. 291, 292) brachiopod-bryozoan analogy. Next below was the hypostegal (another brachiopod term) coelom. The presumed functions of this layer will be discussed subsequently. Next came the inner mantle epithelium, which deposited the laminated, outer skeletal material of the peripheral zone. Continuous with the mantle, the zooidal epithelium (forming the outer surface of the zooid sitting in the zooecial tube) enclosed the stomach, caecum, or gut. The digestive tract is illustrated as U-shaped, as in the modern bryozoans.

As the rhabdomesid zooid drew back into its zooecial tube during retraction, the cuticle was drawn into the vestibule, perhaps closing it off. This would have been an excellent defense against small predators, as they could not have gotten past this cuticular barrier to attack the soft tissues of the zooid. Also, during retraction, the hypostegal coelom was necessarily thinned as it too was drawn into the vestibule.

Zooidal retraction is of two kinds in the living ectoprocts, either colony-wide, where all the zooids retract, or individual, where each zooid retracts independently. Both may be responses to threatening circumstances. Observations made on recent specimens by CUFFEY (personal communication, 1968) indicate that these threatening situations may be as minor as suddenly casting a shadow over the colony or disturbing the surface of the water with a small instrument. Other threats of a more serious nature are obvious enough that I do not need to detail them.

Threats to the individual rhabdomesid zooid were probably rare. However, since the small ramose zoaria of the rhabdomesids did not bear support structures, falling over or dislodgement—a threat to the entire colony—was probably commonplace. This would have resulted in one surface of the zoarium being in contact with the substrate, preventing the zooecia on that side from being utilized in food-gathering. Degeneration and regeneration are common in modern ectoprocts. When the rhabdomesid colony fell onto its side, the zooids so trapped beneath may have degenerated into a "resting stage." Should the colony

have been rolled over subsequently, the zooids could have regenerated into active, food-gathering members of the colony again. This speculation is supported to some extent by the observation that there are fewer laminae in the peripheral zones on the side of those zoaria judged by me to have been lying "down" (that is, against the substrate or aginst an adjoining surface).

Another possibility is that during reproduction, the rhabdomesid zooids involved in this function could have withdrawn into their zooecial tubes. The colony should then have nurtured these zooids, until the reproductive phase had ended or degeneration-regeneration was completed, by communication through the hypostegal coelom. Perhaps muscle strands were anchored to the tips of the acanthopores to open and close interzooecial communication for the duration of such episodes, although this is admittedly completely speculative.

Figure 11 shows how new zooids may have been formed, and the relationship of the tissue layers to skeletal wall construction and zooid formation. The cuticle extended over the entire growth tip. The zooidal epithelium established the inner skeletal walls of the new zooecial tube, while the outer mantle epithelium differentiated into the primordial polypide. At that stage, no laminated skeletal wall was yet in evidence at the most distal extremity. In slightly earlier-formed more proximally located zooecia, we can see progressively more laminae at the abaxial end of the zooecial wall; the most proximal (and thus oldest) zooecial tube shown has many laminae. The stages of zooid differentiation are adapted from HYMAN (1959, fig. 134) and are shown as a sequence from newest-formed (most distal zooecial tubes) to fully mature (most proximal zooecial tube shown). Evidently, full development of the interapertural portions of the peripheral zone was not initiated until the rhabdomesid zooid was fully mature.

VARIABILITY AMONG WREFORD RHABDOMESIDAE

VARIABILITY, STABLE TAXONOMIC CLASSIFICATION, AND NUMERICAL ANALYSES

A taxonomic system must take into account as much of the total morphologic variability of a species or other taxon as is possible, in order to be reasonably stable and not subject to frequent capricious changes. By having followed this principle for two ramose cryptostome genera, I believe that I will have contributed ultimately to the stability of future classificatory studies of bryozoans. CHEETHAM (1968) did this for the cheilostome *Metrarabdotos*. CUFFEY (1967) did this for the trepostome *Tabulipora*. HOROWITZ (1968) did this for the cystoporid *Actinotrypa*. FOERSTER (1970; also FOERSTER & CUFFEY, 1970, in preparation) did this for the modern cyclostome *Crisia*. These papers satisfy a critical need, a need to develop a clear understanding of intraspecific variability among bryozoans in order to establish stability in the classification of the major bryozoan groups. The present study, the first extensive and thorough examination ever made of rhabdomesid cryptostomes, contributes this kind of information for one of the important major kinds of bryozoans; it will, moreover, hopefully stimulate similar future work on this and other cryptostome bryozoan groups.

As previous workers on tubular bryozoans have shown, these bryozoans tend to be rather highly variable in their morphology (CUFFEY, 1967; HOROWITZ, 1968; FOERSTER, 1970). Inspection of the plates accompanying this present paper and of the relatively large coefficients of variation exhibited by most of the numerical morphological characters studied herein (Tables 7 and 8) indicate that the Wreford rhabdosomesids also display considerable intraspecific variability. This conclusion is reinforced by the previously discussed fact that intraspecific variants within *Rhombopora lepidodendroides* could have been assigned to four different genera (*Rhombopora, Rhabdomeson, Saffordotaxis,* and *Nicklesopora*) as traditionally recognized. Now that this present paper has shown the actual extent of intraspecific variability among the Wreford rhabdomesids, future taxonomic concepts utilized for these and similar bryozoans can be made to coincide more closely with realistic biologic species concepts (CUFFEY, 1967, p. 65). Thus, future classifications of these bryozoans can be far more stable than past classifications, which have usually been highly artificial and frequently based on one or a few characters studied in only a few specimens.

However, the Wreford rhabdomesid species do not seem to exhibit quite as much variability as does the Wreford trepostome species *Tabulipora carbonaria,* studied extensively by CUFFEY (1967). This may result from the fact that the rhabdomesid colonies are much smaller and more simply constructed than are the trepostome colonies, and thus do not possess the potentiality for quite such extensive variability.

The Coefficient of Variation (CV) has been widely used to assess the potential value of a morphological character for taxonomic work (HOROWITZ, 1968; CUFFEY, 1967; CHEETHAM, 1968; MATURO & SCHOPF, 1968; FOERSTER, 1970; FOERSTER & CUFFEY, 1970, in preparation). HOROWITZ, CUFFEY, and FOERSTER utilized hundreds of measurements in their studies on colonially aggregated tubular bryozoans. So have I. CHEETHAM, MATURO, and SCHOPF, on the other hand, suggest that ten to twenty measurements are adequate to accurately assess CV in

cheilostome bryozoans. Since CV is obtained by dividing the standard deviation by the mean, then multiplying by 100, CV is somewhat dependent upon sample size when small samples are used. That is, the larger is the size of the sample, the more likely it is that variants in the "tails" of the distributions will be included; thus, standard deviation empirically often tends to increase (up to a limiting value) as sample size increases from very small up to adequate numbers (note also RICHARDSON, 1944, p. 450).

CUFFEY (1967) found that very few of his CV calculations for *Tabulipora carbonaria* were less than 10, some were between 10 and 20 and most ranged from 20 up to 400 and beyond. In contrast, cheilostome workers have suggested that the CV forming the dividing line between taxonomically useful characteristics and taxonomically less useful ones, is about 10. This paper, along with those of the other workers in tubular bryozoans mentioned above suggests that the boundary should be higher, perhaps at a CV of 20.

Most cheilostome bryozoan measurements are made upon individual zooecia. Many of the measurements of the tubular bryozoans are, in contrast, parameters of entire colonies. I suggest that, based on numbers generated by me, CUFFEY (1967), HOROWITZ (1968), and FOERSTER (1970), we can classify numerical morphological characters into four groups according to their CV's. These four groups are summarized in Tables 9 and 10, and may be examined in more detail in the tables of Appendix B.

TABLE 9. *Classification of Numerical Morphological Characteristics into Four Groups Based Upon Coefficients of Variation (CV) Computed for* Rhombopora lepidodendroides.

GROUP	CV	MEMBERS
Group I	less than 20	MZAD, Z2
Group II	20 - 30	MMUW, MNUW, NMA, MMAW, NMU, ZA, Z1
Group III	30 - 40	MMSP, AZD, IWT, NRIW
Group IV	40 - infinity	DTZ_2, TP, NMSP, MWZ

TABLE 10. *Classification of Numerical Morphological Characteristics into Four Groups Based upon Coefficients of Variation (CV) Computed for* Syringoclemis wrefordensis.

GROUP	CV	MEMBERS
Group I	less than 20	MZAD
Group II	20- -30	Z2, ZA, MWZ, IWT, MMAW
Group III	30 - 40	MMSP, AZD, TP, NMSP, NMA
Group IV	40 - infinity	ZI, DTZ_2

Group I, with CV less than 20, consists of characters of the highest potential value for bryozoan taxonomy. Group II, with CV from 20 to 30, is comprised of characters of moderately high potential value. Group III, with CV from 30 to 40, contains those characters of low potential value. Group IV, with CV 40 to infinity, is the group of parameters with the lowest potential value for taxonomy. Inspection of these tables indicates that some of these characters, such as MZAD and Z2, which seem potentially valuable in future rhabdomesid taxonomic studies were also suggested as having potential taxonomic value among trepostomes (CUFFEY, 1967, p. 66).

Many currently active bryozoan workers use numerical or statistical summaries to describe their taxa more precisely than paleontologists traditionally have. Such numerical data is especially helpful in describing the extent of intraspecific morphologic variability, for example.

For numerical characters whose statistical distributions are normal or nearly so, mean and standard deviation values suffice to describe the shape of their distribution. For nonnormally distributed parameters, other statistics are required. ANSTEY & PERRY (1970) urge that bryozoan studies also include at least skewness and kurtosis for more complete descriptions of nonnormal distributions. Coefficients of variation, as discussed above, can often be determined from published mean and standard deviation values.

The object of most studies is to differentiate between taxa. The object of this present study was to establish, as completely as possible, a set of statistics which would enable future workers in the ramose cryptostomes to identify their specimens with greater confidence by pointing out what characters are most likely to be of taxonomic value. For example, comparing a group of specimens which are seemingly related to *Rhombopora lepidodendroides* will be greatly accelerated by first making a few observations of parameters with Group I or Group II CV, and then comparing their preliminary statistics with mine from the Wreford rhabdomesid species. Otherwise, considerable effort could be needlessly expended on such things as elaborately designed sampling schemes or factor-analytic techniques requiring large quantities of numerical data, when instead a few observations of carefully selected characters could tell the worker much of what he desires to know.

Figures 12 and 13 compare the statistical distributions of four characters (Z1, Z2, MMAW, and NMA) in each of the two Wreford rhabdomesid species. The CV Groups of Z1 and Z2 for *R. lepidodendroides* are II and I, respectively, and for *S. wrefordensis* IV and II, respectively. MMAW for both species is CV Group II. NMA for *R. lepidodendroides* is Group III, but Group II for *S. wrefordensis*. It is evident that mean, CV, and standard deviation do not adequately express differences among statistical distributions; I therefore, strongly agree with ANSTEY & PERRY (1970), and HOROWITZ (1968), that other statistics describing distribution of variates should be presented.

The tables of Appendix B contain all statistical param-

eters commonly considered useful in describing statistical distributional properties of biological populations (Anstey & Perry, 1969, 1970; Cuffey & Perry, 1964; Horowitz, 1968; Simpson, Roe & Lewontin, 1969). These tables thus supplement the verbal descriptions of the Wreford rhabdomesids contained in the text of this paper.

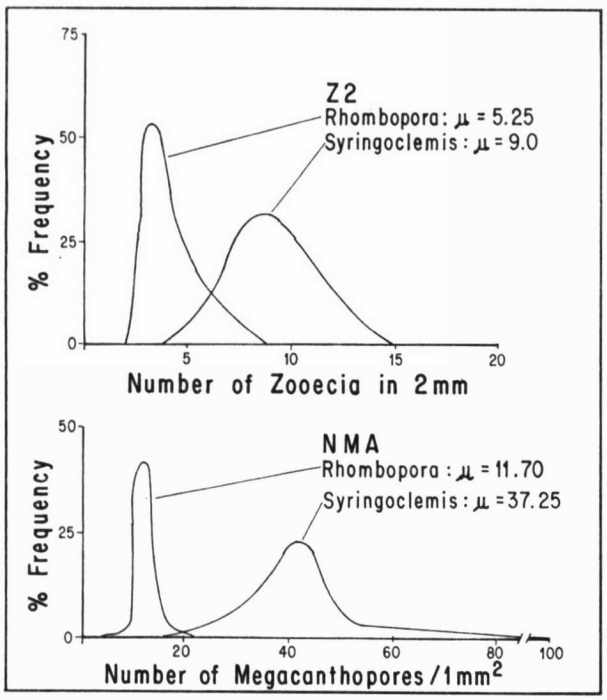


Fig. 12. Frequency distributions computed from all observations on the characters Z2 and NMA made on the Wreford Megacyclothem specimens of *Rhombopora lepidodendroides* and *Syringoclemis wrefordensis*.

In spite of the foregoing, however, some criticism has been made of the use of statistical description or inference in the evaluation of fossil assemblages (Ross, 1967). These criticisms warrant some general comments, inasmuch as their scope is rather wide.

Ross (1967, p. 404) asks whether suites of fossils, or observations on such fossils, like my Wreford rhabdomesids "constitute a random sample from a fixed [contemporaneous] population."

Previous stratigraphic work on the Wreford Megacyclothem has indicated that all samples taken from any one of the several horizons within these rocks can be regarded as essentially synchronous or contemporaneous geochronologically. This fact, I believe, answers part of her criticism.

The other question which Ross raises, that of randomness, is also difficult for me to see as a valid objection. Usually, small samples (specimens in a museum collection, or specimens from one or a few outcrops) are all that is available for study. In such cases, it seems unreasonable to abandon completely statistical description, or to use statistical methods filled with elaborate disclaimers, to deal with the specimens. Given the number of samples, number of measures, mean, mode, range, standard deviation, coefficient of variation, skewness, and kurtosis, the reader can make good use of such data, for example, developing his own ideas concerning which specimens he would like to compare with those described or cited.

Moreover, Horowitz (1968, p. 365-366) stated:

"I suspect that stratigraphic fossil collections are by their nature random. The opportunities to observe are probably random with respect to the total outcrop of a unit and even to its total areal extent. Such inferences about randomness are hardly more suspect than inferences about gene flow in interbreeding populations as deduced from the fossil record. Both are reasonable 'intuitive' inferences that are based on the present state of knowledge."

In addition, the availability of samples from the Wreford Megacyclothem is subject to such random operations as the amount of rainfall, the number of freeze-thaw cycles of the previous winter, the amount of vegetation overgrowing the outcrops and exposures, and the cut and fill activities of the highway department.

Also relevant to this discussion is the fact that animals are not randomly distributed in nature. One would not,

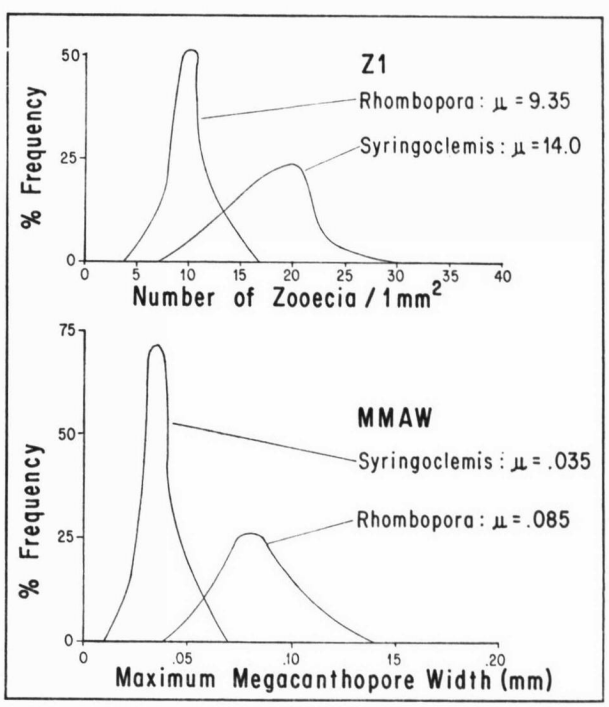


Fig. 13. Frequency distributions computed from all observations on the characters Z1 and MMAW made on the Wreford Megacyclothem specimens of *Rhombopora lepidodendroides* and *Syringoclemis wrefordensis*.

for example, include southern Alaska in a sampling plan designed to collect data on the fine details of alligator distribution, because we know from previous work that there will be no native alligator population in Alaska. Animals are where they are because they occupy specific environmental niches. Had I known in advance which rock units would yield the most information on the Wreford rhabdomesids, more elaborate sampling could have been designed beforehand. However, I knew only that these bryozoans probably preferred normal saline waters; since I knew nothing else about their environmental preferences, I had to sample the Wreford rocks as comprehensively as possible. By sampling every rock type at each exposure, and by drawing from collections made earlier by CUFFEY (1967) in this same way, I feel that my sampling was essentially random, in the sense that "random" simply means that every member of a set has an equal chance of being chosen.

Another numerical technique, though not strictly statistical in the same sense that the methods discussed above are, is cluster analysis. When used to group or cluster similar objects described in numerical terms, cluster analysis techniques can be potentially quite helpful in classifying a large number of morphologically variable objects like rhabdomesid fossils.

In the section on methods I have previously discussed the technique of cluster analysis as applied to the Wreford rhabdomesids. The result of this application is a large dendrogram (Fig. 9), which represents a strictly phenetic grouping of these fossils according to their similarities. This phenetic grouping by itself does not constitute an acceptable final systematic classification, because paleontological systematics ultimately involves evolutionary or historical data, as well as morphological phenetic data. However, such phenetic groupings as this can serve as a very useful first step in developing a taxonomic classification for fossil organisms, as well as for indicating the overall extent of variability shown among the forms so classified.

Since my main goal in this paper has been to attempt as complete an understanding as possible for the two Wreford rhabdomesid species, I made every effort to incorporate all the data I had gathered for this paper into this cluster analysis, striving for a polythetic classification. Monothetic classifications, classifications based on single-character differences between genera and species of genera (for example *Rhabdomeson, Saffordotaxis,* and *Nicklesopora,* as discussed previously) are the antithesis of my efforts.

In the Wreford rhabdomesid dendrogram (Fig. 9) each "tic" represents one sample (one Wreford rhabdomesid colony). In addition, samples labeled include TYPS, an imaginary "typical" *Syringoclemis wrefordensis* assembled by coding the mean values of all parameters for that species, and TYPR, an imaginary "typical" *Rhombopora lepidodendroides* assembled as TYPS was. The other labeled samples (A001 to A004) are the four members of the type suite loaned to me by the United States National Museum of the Smithsonian Institution (because of space limitations, and in the interest of clarity, individual specimen numbers are not indicated).

Two very tightly clustered groups are evident in the dendrogram (Fig. 9). The lower group of only 26 specimens is composed entirely of specimens identified as belonging to *Syringoclemis wrefordensis.* The upper, larger, group is comprised entirely of *Rhombopora lepidodendroides* colonies. This dendrogram was constructed using the unweighted pairing method and Jaccard's coefficient of association (BONHAM-CARTER, 1967, p. 2-3).

It seems reasonable to conclude, based on Figures 8 and 9, that the associative level for the family Rhabdomesidae, which is where genera cluster into the family level, is about 0.58. Another conclusion drawn from the dendogram is that both *R. lepidodendroides* and *S. wrefordensis* in the Wreford Megacyclothem are internally quite closely comparable (0.80 to 0.85), when described by the parameters used here for the cluster analysis.

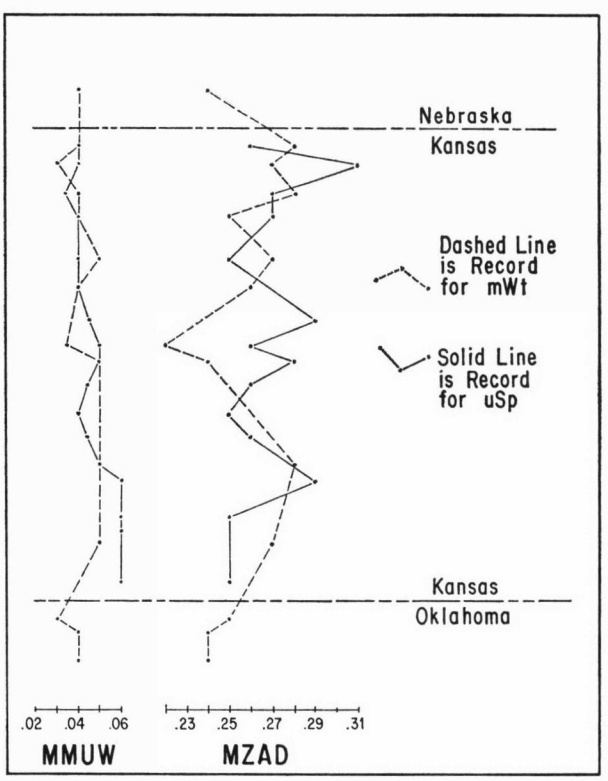


FIG. 14. Clinal (geographic) variation in the means of MMUW and MZAD for specimens of *Rhombopora lepidodendroides* collected from the middle Threemile and upper Speiser from localities in Nebraska, Kansas, and Oklahoma.

BONHAM-CARTER's admonition "that different classifications can be obtained from the same data," therefore, cluster analysis techniques should only "be used as a data reduction tool, to give computational *aid* for classification" (BONHAM-CARTER, 1967, p. 8, emphasis his) is worth heeding. Consequently, only the broad conclusions drawn above are suggested here.

However, I think that the dendrogram may also serve as a valuable test of the hypothesized generic difference between *Rhombopora* and *Syringoclemis*. In general, in samples where several genera of rhabdomesids may be present, the clustering values obtained here may be of value in suggesting their classification.

CLINAL AND EVOLUTIONARY VARIABILITY

Because only 84 *Syringoclemis wrefordensis* were available for study, and because they were not widely distributed, only *Rhombopora lepidodendroides* was used in the evaluation of clinal (or geographic) variation among the Wreford rhabdomesids. Figure 14 summarizes the median value of two characters (MMUW and MZAD) at several localities in both the upper Speiser and middle Threemile calcareous shales. Comparable plots were made for other characters, and the results were similarly ambiguous. Consequently, I conclude that clinal variation was not exhibited in the Wreford population of *R. lepidodendroides*. CUFFEY (1966, 1967), using the same technique, was able to show gradual clinal changes in *Tabulipora carbonaria* in a north-south direction across Kansas in the Wreford Megacyclothem.

Again, for *Tabulipora carbonaria,* CUFFEY (1966, 1967) was able to show progressive change as he evaluated the means of several characters in a stratigraphically vertical direction. I computed the means for four morphologic characters (Z1, MZAD, MMAW, MMUW) of *Rhombopora lepidodendroides* for the five widespread calcareous shale units in the Wreford Megacyclothem, and plotted them stratigraphically (Fig. 15).

The information derived from this appears to be equally as ambiguous as that gathered from plotting the data for the clinal (geographic) variation study just discussed. No directed evolutionary or stratigraphic variability characterizes successive populations of *Rhombopora lepidodendroides* within the Wreford Megacyclothem.

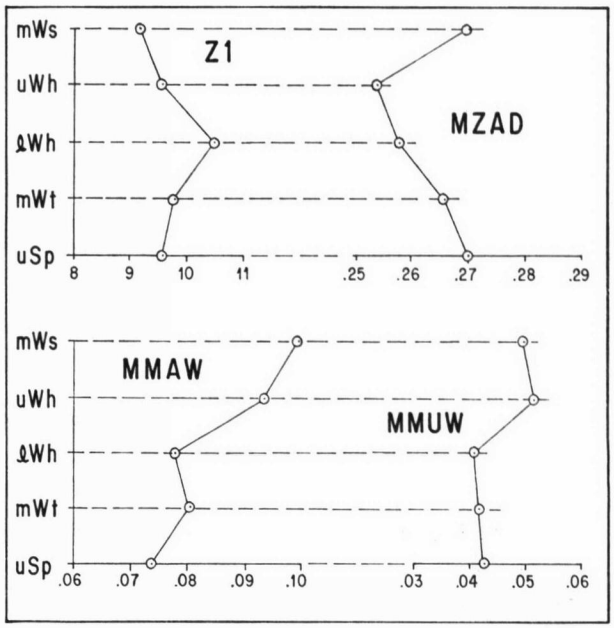


FIG. 15. Microevolutionary (stratigraphic) variations in the means of four characters (Z1, MZAD, MMAW, MMUW) shown in specimens of *Rhombopora lepidodendroides* collected from the five widespread Wreford Megacyclothem calcareous shales.

At a more long-ranging scale than the megacyclothem alone, however, *Rhombopora lepidodendroides* does not display significant evolutionary variation or change. In the dendrogram (Fig. 9), the colonies labeled A001 through A004 are the type suite of *R. lepidodendroides*. The type horizon of *R. lepidodendroides* is the Wabaunsee Group (Upper Pennsylvanian, Virgilian). These types cluster in the center of the dendrogram and cannot be readily differentiated from the Wreford Megacyclothem examples of *R. lepidodendroides,* even though they are considerably more ancient biostratigraphically. Consequently, this species seems to have been a rather conservative one, retaining its average morphologic condition essentially unchanged for a significant length of time.

In summary, assembling this information yields the conclusion that *Rhombopora lepidodendroides* did not vary systematically, either evolutionarily (from Upper Pennsylvanian to upper Lower Permian), microevolutionarily (through the time represented by the Wreford Megacyclothem), or clinally (at least during the Wreford).

PALEOECOLOGY OF WREFORD RHABDOMESIDAE

WORLDWIDE PALEOZOOGEOGRAPHY OF LATE PALEOZOIC RHABDOMESIDAE

On a worldwide basis, the Rhabdomesidae can be seen to be well-distributed in the marine, shallow-shelf facies of Upper Paleozoic rocks, as is shown by Figures 16 and 17. In preparing these figures, only the highest stratigraphic occurrence is recorded for any one report. That is, the half-black circle at 80°15′ North, 16°30′ West, Holm Land, Greenland, in Figure 18 represents a

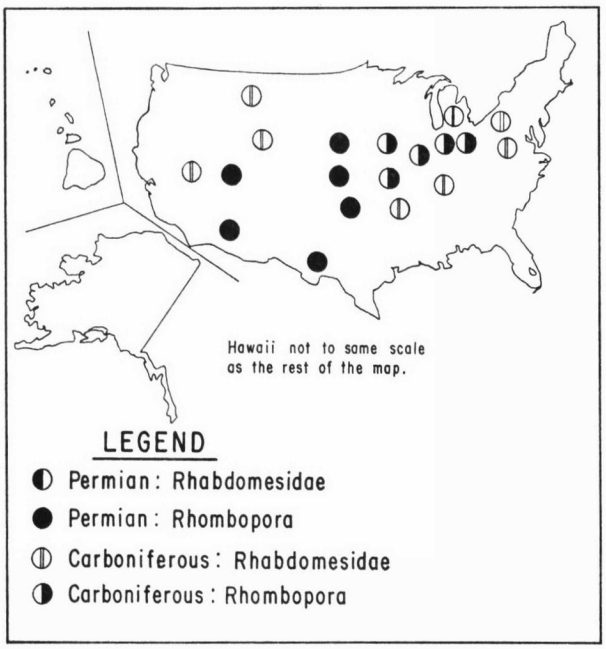


FIG. 16. Paleozoogeographic distribution of the family Rhabdomesidae in the United States in the Carboniferous and Permian.

report of Permian Rhabdomesidae but not *Rhombopora* (Ross & Ross, 1962). The unshaded, barred circle in Bolivia (BASSLER, 1936) represents Carboniferous Rhabdomesidae but, again, not *Rhombopora*. Had the first (Greenland) been a Permian *Rhombopora* citation, the circle would have been all black. Had there been found a reference to a Permian rhabdomesid in Bolivia, this report would have superseded the first, and the circle would have been half-black.

In Appendix C, I have listed the best information available on the stratigraphic occurrences of the various rhabdomesid species, and recorded there the systems, series, stages, and even formations when that information was obtainable. In order to show the geographic distribution of the fossil Rhabdomesidae more clearly, I have drawn (Fig. 18) the continents and principal landmasses to the same scale, but to decrease the amount of oceanic space and to increase the accuracy of point location, I have moved the landmasses closer together.

It is appropriate to state here that the importance of this family for an understanding of the bryozoans, particularly cryptostomes, and for colonial organisms in general, and even for all marine communities of the Paleozoic—particularly here, near the Paleozoic-Mesozoic boundary crisis—is clearly evidenced not only by the wide

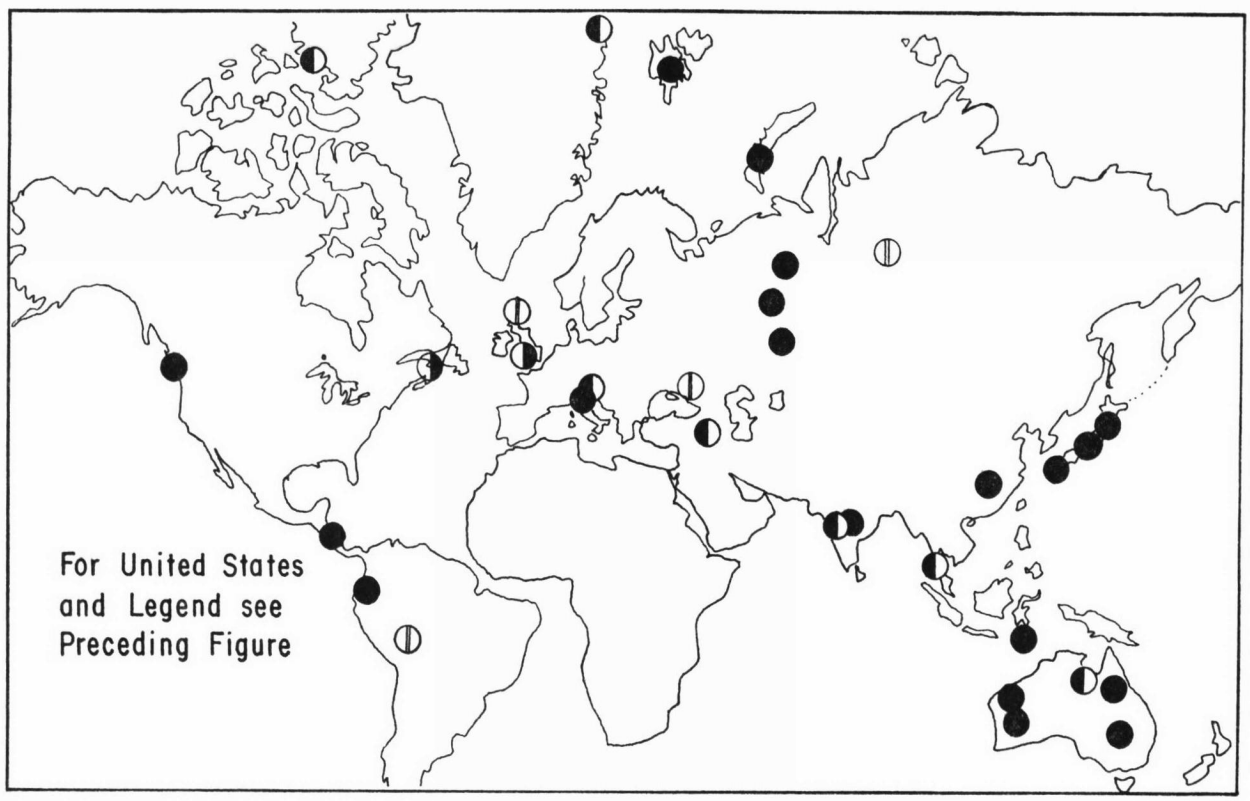


FIG. 17. Worldwide paleozoogeographic distribution of the Rhabdomesidae in the Carboniferous and Permian.

distribution of the family, but also by its excellent coverage in the literature and by its abundance in the rocks of the world.

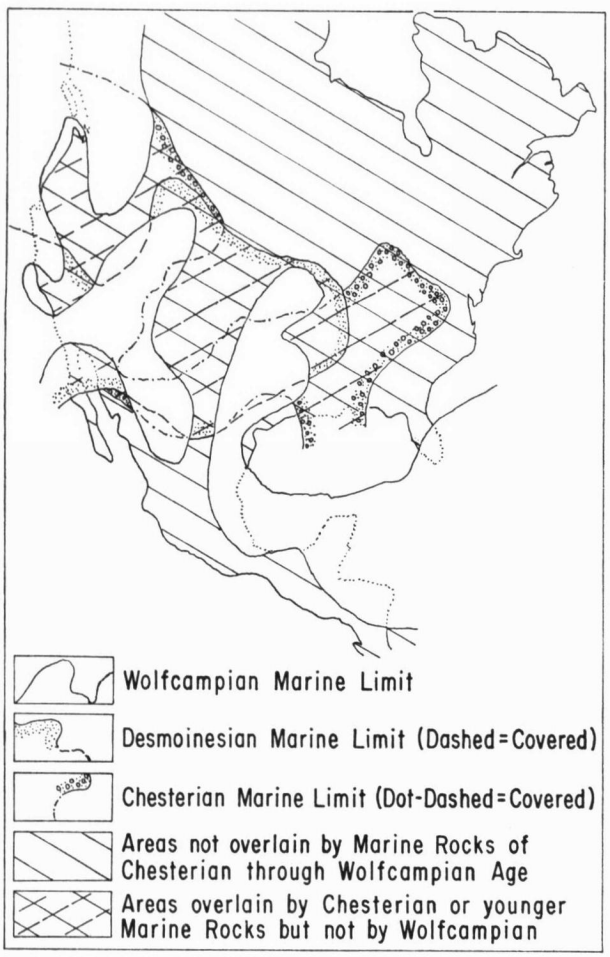


FIG. 18. Distribution of Upper Paleozoic marine rocks in North America (after Dunbar, 1960).

NORTH AMERICAN AND WREFORD PALEOZOOGEOGRAPHY OF LATE PALEOZOIC RHABDOMESIDAE

Figure 18 illustrates an important, perhaps the most important, point involved in the classification and interpretation of North American Permian faunas. In the Mississippian, an extensive marine transgression flooded North America. In this sea, invertebrates flourished, including ten rhabdomesid genera, five of which were new. Marine, shallow-water, benthonic habitats were highly ubiquitous on the North American continent during this period; burgeonings and outspreadings in the shelled invertebrates were commonplace at this time.

During the following Pennsylvanian period, the epeiric seas began to become restricted, smaller, locally deeper, thus limiting the number of shallow-water environmental niches. A concomitant decrease in the rate of evolutionary diversification therefore characterized Pennsylvanian marine faunas. For example, only three new genera of rhabdomesids appeared, as against three extinctions within the group. As is so often the case in the geologic record, restriction of the epicontinental seas resulted in restricted faunas with restricted diversity.

The Mississippian seas which retreated from Pennsylvania, Michigan, and Ohio were replaced to a lesser extent in the Pennsylvanian. The Pennsylvanian seas continued the retreat, forcing their restricted marine invertebrate faunas to become condensed or collapsed back into Illinois, Iowa, Missouri, Nebraska, Kansas, Oklahoma, Texas and New Mexico. That this retreating was discontinuous, in fact cyclic, is indicated by widespread development of cyclothems in the Pennsylvanian and Permian from Texas to Pennsylvania. The rocks of these cyclothems record the pulses of the withdrawing seas.

An ecologic principle (GAUSE, 1934; HARDIN, 1960) known as the "competitive exclusion principle" states that "No two species can coexist at the same locality if they have identical ecological requirements" (MAYR, 1963, p. 68). Generally, however, two closely related animals newly brought together have the ability to make noncompetitive use of their common habitat. For example, a common littoral gastropod of Hawaii, *Conus,* has twenty species living in the same habitat. All twenty occupy ecologic niches of slightly differing nature. On the other hand, intertidal barnacles (CONNELL, 1959) compete more stringently, and there is usually only one species per habitat, and always one species per ecologic niche. When two species utilize the identical resources (as do the barnacles) of an environment, one of these species proves superior and eventually excludes the other species.

In the Wreford Megacyclothem, *Rhombopora lepidodendroides* apparently eventually excluded *Syringoclemis wrefordensis. Rhombopora* may have always been evolutionarily "vigorous," since fully twenty percent of the more than 200 rhabdomesid species known to me are species of *Rhombopora,* while less than one percent are *Syringoclemis.* However, this argument may perhaps be fallacious. That is, there may be no reason to presume that the "vigor" of *Rhombopora,* in terms of its competitive potential, was any greater than that of *Syringoclemis.* However, some numerical evidence bearing on this question is at hand. Of the 84 *S. wrefordensis* specimens (84 out of the 1,027 Wreford rhabdomesids examined, 943 or 92% being *R. lepidodendroides*), 63 came from the upper Speiser calcareous shale, the lowermost normal marine shale in the Wreford Megacyclothem. Of these 63, nineteen came from a small area in southern Kansas (CY15 and CY43) and nineteen from a some-

what larger (though still small) area in northern Kansas (ML03 and PT09). These two small redoubts are interesting in terms of the ideas outlined above in the discussion of the competitive exclusion principle. In the southern redoubt, *Syringoclemis* comprises 100% of the rhabdomesid cryptostomes present. In the northern redoubt, *Syringoclemis* makes up 73% of the rhabdomesid fauna. Immediately south of the southern redoubt and immediately north of the northern redoubt, percentage values of *Syringoclemis* (percentage of total rhabdomesid cryptostomes present) fall to zero. Figure 19 summarizes this information by percentage contours. Basically, the figure shows two pockets of high *Syringoclemis* concentration on the margins of the Wreford sea, flanked toward shore by abrupt zero percent density, and flanked into the basin by more or less evenly decreasing gradational changes. It is interesting to note as an aside that the location of the Greenwood Shoal lies immediately south of the minimum contour position.

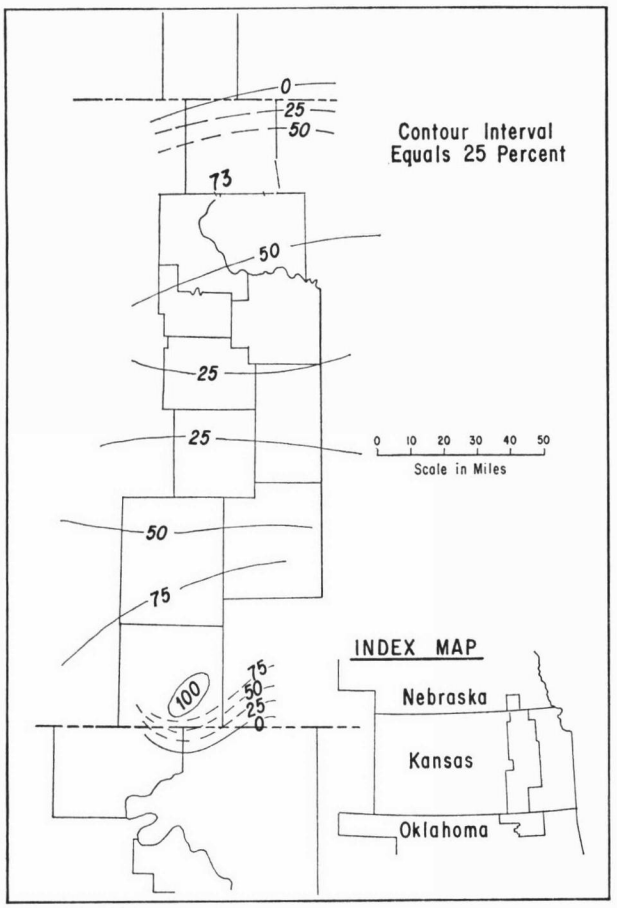


FIG. 19. Distribution of *Syringoclemis wrefordensis* in the upper Speiser calcareous shale. Dashed contour lines are hypothetical. The two closed contours represent the two redoubts as discussed in the text.

Continuing upward in the section (and, therefore, in time), the number of *Syringoclemis wrefordensis* specimens decreases steadily, though erratically. No examples are known from the Threemile Limestone Member. Three are known from the lower and 15 from the upper Havensville. One specimen is known from the Schroyer, and, finally, none at all are known from the Wymore.

As MAYR (1963, p. 210-214, 237-240) points out, a change in population size influences selection pressures. In rapidly increasing populations, selection pressures are diminished. In populations that are rapidly decreasing in size, there is a concomitant rapid rise in selection pressure. In summary, then, I suggest that the collapsing-back of animal populations caused by the retreating late Paleozoic seas and by the heightened competition for specific ecological niches in the limited habitats resulted in exclusion of all but a few species by Permian times. CUFFEY (1966, 1967) has shown that this resulted in there being only one trepostome bryozoan species present in the Wreford Megacyclothem. My study shows that only one rhabdomesid cryptostome species, *Rhombopora lepidodendroides,* is present at the close of the last regressive phase of the Wreford Megacyclothem; that species seems to have excluded competitively the only other rhabdomesid cryptostome species, *Syringoclemis wrefordensis,* during the span of Wreford time.

OBSERVATIONS ON PALEOECOLOGY OF THE WREFORD RHABDOMESIDAE

The two genera of rhabdomesid cryptostomes, *Rhombopora* and *Syringoclemis,* show no observable directed vertical (evolutionary or stratigraphic) or lateral (clinal or geographic) changes within the Wreford Megacyclothem. The eventual exclusion of *Syringoclemis wrefordensis* by *Rhombopora lepidodendroides* is interpreted to have occurred solely due to the two Wreford rhabdomesids seeking the same ecologic niche, rather than being due to any specific environmental factor operating against one *(S. wrefordensis)* and not the other *(R. lepidodendroides).*

Moreover, no systematic variability is evident when comparing the morphologic characteristics of several conspecific rhabdomesid colonies, each one taken from a different Wreford rock type, unlike the situation in *Tabulipora carbonia* (CUFFEY, 1967, p. 65). For example, I could detect no consistent morphological differences between *Rhombopora lepidodendroides* colonies occurring in calcareous shales and those in grayish-yellow mudstones. This situation is not surprising, however, in view of how much alike the various Wreford depositional environments may have been so far as critical ecological factors (like substrate) were concerned (CUFFEY, 1967, p. 25-26, 77).

Bottom conditions in Kansas during Wreford time are interpreted as usually being soft muddy substrates affected

by no or low turbulence. Such features as graded beds, ripple marks, or crossbeds are rare in the Wreford Megacyclothem (HATTIN, 1957; CUFFEY, 1966, 1967, personal communication 1970; this report). In addition, the excellent preservation of delicate spinose projecting elements also suggests very low energy for bottom conditions in the Wreford sea. Certainly, such delicate features would be instantly destroyed upon being moved about upon the bottom to even a very minor extent. Simply falling over onto a firm substrate, then rolling (let alone saltating), would be more than sufficient to destroy at least some of these beautifully preserved features.

The majority of the Wreford rhabdomesids, in fact the majority of all Wreford bryozoans, are known from the megacyclothem's widespread calcareous shales. Consequently, I infer that the rhabdomesid cryptostomes of the Wreford Megacyclothem preferred shallow waters (under 50 feet) of normal marine salinity and far from shore. However, many of them could also tolerate slightly less saline conditions and slightly more nearshore conditions, as evidenced by their occasional occurrences in grayish-yellow mudstones. A fair number of Wreford *Rhombopora lepidodendroides* are found as constituents of the grayish-yellow mudstones and, since the grayish-yellow mudstones are commonly interpreted as having been deposited in slightly brackish marine waters, in a rather shallow and nearshore environment, it can be inferred that *R. lepidodendroides* tolerated a moderate range of salinity. On the other hand, *Syringoclemis wrefordensis* is known only from one specimen in grayish-yellow mudstones and thus was presumably more stenohaline.

SUMMARY AND CONCLUSIONS

1) Techniques of many types are applied in this study. All techniques that I employed satisfy two criteria. The first is reproducibility by other paleobryozoologists working on similar ramose groups; the second is wide-ranging applicability to all bryozoan groups through ease of use or calculation. Collection techniques were designed to yield comprehensive and unbiased samples; they follow the stratigraphic interpretation of CUFFEY (1966, 1967) and HATTIN (1957). Extension and modification of the cellulose acetate peel technique was made to accommodate the small size of the specimens of the Wreford Megacyclothem rhabdomesids. Statistics based on some 15,000 measurements were calculated by use of the IBM System 360/67 computer. Modification of BONHAM-CARTER's (1967) computer program permitted calculation of a cluster analysis for the family Rhabdomesidae and for Wreford specimens of the two genera *Rhombopora* and *Syringoclemis,* resulting in dendrograms.

2) A set of numerical characters based on the rhabdomesid cryptostomes of the Wreford Megacyclothem is defined for use in the description of ramose cryptostomes in general. Some of these are new, others are based on previous work on other bryozoans. Each character is given an abbreviated symbol. These symbols are suggested as part of an effort to encourage constancy in future bryozoan descriptions.

3) New stratigraphic information indicates that exceedingly rapid facies changes occur within the Wreford Megacyclothem at the Kansas-Oklahoma border and southward into Oklahoma with all lithologies quickly passing into continental redbeds. Although Cretaceous and Pleistocene cover obscures most of the Wreford Megacyclothem in southern Nebraska, exposures indicate that the shore of the Wreford sea was fairly far south in Nebraska, perhaps a few tens of miles north of the Nebraska-Kansas border. One new lithotype (tan quartzose sandstone) is added to those already defined for the Wreford Megacyclothem (HATTIN, 1957; CUFFEY, 1966, 1967).

4) The very close similarity of the genera *Rhabdomeson, Saffordotaxis,* and *Nicklesopora* to *Rhombopora*—in part emphasized by examination of the Wreford rhabdomesids—suggests that those three genera should be synonymized with *Rhombopora.* Moreover, these three genera are monothetic genera and only differ from *Rhombopora* on the basis of one character each; in accordance with modern taxonomic practices, monothetic taxa are normally to be suppressed. *Rhombopora* is the oldest (1872) of these four genera, as well as the best-known genus of the Rhabdomesidae.

5) *Syringoclemis wrefordensis* is proposed as a new species, differing from the only other species of *Syringoclemis, S. biserialis* GIRTY, 1911, a Mississippian (Chester) form, in many respects. The concept of the genus *Syringoclemis* is thus expanded to include solid ramose zoaria as well as epithecate zoaria. A holotype and two paratypes are designated.

6) The skeletal morphology of the two Wreford rhabdomesid species, *Rhombopora lepidodendroides* and *Syringoclemis wrefordensis,* is thoroughly described for the benefit of workers interested in comparing other bryozoan species with them.

7) Based on TAVENER-SMITH's (1969) and WILLIAMS' (1968) work, the laminae of the peripheral zone in the Wreford rhabdomesids are interpreted as indicating diurnal periodicity. Counts on a few peripheral zones indicate that some of the Rhabdomesidae of the Wreford Megacyclothem were as much as 18 months to two years old and more at death.

8) Mesopores and acanthopores are present in the

rhabdomesid cryptostomes of the Wreford Megacyclothem but are not believed to be analogous to features of the same name and general appearance in the Trepostomata. Considerations of the size of these features, their location in the zoarium, their microstructure and skeletal relationships, and their presumed functions led to this conclusion.

9) Structures exactly fulfilling the criteria for hemisepta (either inferior or superior hemisepta) are judged to be absent from the rhabdomesid cryptostomes of the Wreford Megacyclothem. Similar structures are rarely present in a few specimens; however, on the basis of their position in the zooecium, percentage paucity, and morphology, they are not considered to be true hemisepta.

10) The first reconstructed rhabdomesid cryptostome polypide is offered. The reconstruction is based on an interpretation of the skeletal morphology of the Wreford rhabdomesids and is in large part an application of TAVENER-SMITH's (1969) concept of the soft parts of the Fenestellidae. Some conclusions on reproduction, degeneration-regeneration, growth, and colony defense are offered based on the reconstructed zoarial tissues.

11) Studies of the moderately high morphologic variability displayed by the Wreford rhabdomesid species indicate that some of their numerical morphological characters are potentially highly valuable for future taxonomic work, while others are much less valuable.

12 *Rhombopora lepidodendroides* was found to have varied little or not at all in its average morphologic condition from Virgilian (Late Pennsylvanian) through Wreford (Early Permian) time. Clinal (geographic) variation and microevolutionary (stratigraphic) variation within this species were also found to lack any systematic pattern. The directionless, ambiguous nature of the patterns, yielded by plotting values of numerical characters for the Wreford specimens of *R. lepidodendroides* against time, indicated that the species can be regarded as a rather conservative form.

13) Several aspects of the paleoecology of the Wreford rhabdomesids are discussed. Of particular interest, the competitive exclusion principle is suggested as being responsible for the total replacement of *Syringoclemis wrefordensis* by *Rhombopora lepidodendroides* during Wreford time. This concept is examined on the basis of worldwide, North American, and Wreford evidence. The restriction of late Palezoic seas is suggested as a stringent factor in the operation of natural selection upon marine benthonic animals during this critical period in the earth's history.

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APPENDIX A—SUMMARY OF BULK SAMPLE RAW DATA

Listed for the bulk samples, for all localities not previously so treated by CUFFEY (1966, 1967), are the numerical abundance (abbreviated as Num.Abd.), the percent abundance (abbreviated as Per.Abd.), and the total for each bryozoan zoarial growth form. The symbol "tr" means trace (less than a one percent occurrence). The symbols for the bryozoan morphotypes (ETL, ESL, etc.) have been explained on p. 16-17.

	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
GA03(-B) bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA03(-A) bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Num.Abd.
GA03B bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA03C bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA03D bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA03E bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA03F bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA03G bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA03H bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA03I bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA03J*l*1/2 bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA03Jm1/2 bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA03L*l*1/3 bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA03Lu1/3 bfN PC										
	000	000	000	073	000	000	000	006	80	Num.Abd.
	000	000	000	091	000	000	000	009	100	Per.Abd.
GA04A bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GA04B bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.

	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
GA04JUL/C bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
ML03Jb bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
ML03Jc bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
ML03Jd bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
ML03L*l*1/3 bfN PC										
	001	000	000	053	008	000	000	000	62	Num.Abd.
	002	000	000	085	013	000	000	000	100	Per.Abd.
ML03Lm1/3 bfN PC										
	000	000	000	000	094	000	001	005	100	Num.Abd.
	000	000	000	000	094	000	001	005	100	Per.Abd.
ML03Lu1/3 bfN PC										
	000	000	000	018	131	000	000	000	151	Num.Abd.
	000	000	000	013	087	000	000	000	100	Per.Abd.
ML03O/P bfN PC										
	000	000	000	007	010	000	001	029	47	Num.Abd.
	000	000	000	015	021	000	002	062	100	Per.Abd.
ML03R/S bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
ML03Sm1/3 bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
ML03Su1/3 bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
ML03U bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
ML03JUL/W bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT03Aa bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT03Ab*l*1/2 bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT03Abu1/2 bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT04Cu1/4 bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT04Cu1.Oft. bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT04Ea										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.

	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
PT04EuO.5ft. bfN PC										
	000	000	000	000	007	000	002	007	16	Num.Abd.
	000	000	000	000	044	000	012	044	100	Per.Abd.
PT04Eb bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT04G*l*1/2 bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT04Gu1/2 bfN PC										
	000	000	000	000	008	000	000	008	16	Num.Abd.
	000	000	000	000	050	000	000	050	100	Per.Abd.
PT04J*l*1/2 bfN PC										
	000	001	004	021	006	006	000	017	55	Num.Abd.
	000	002	007	038	011	011	000	031	100	Per.Abd.
PT04Jul1/2 bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT09A/B bfN PC										
	000	000	000	000	000	000	000	001	1	Num.Abd.
	000	000	000	000	000	000	000	099	99	Per.Abd.
PT09C*l*1/3 bfN PR										
	000	000	000	037	035	000	000	008	80	Num.Abd.
	000	000	000	046	044	000	000	010	100	Per.Abd.
PT09Cm1/3 bfN PC										
	000	000	000	036	122	000	000	007	165	Num.Abd.
	000	000	000	022	074	000	000	004	100	Per.Abd.
PT09Cu1/3 bfN PR										
	000	001	000	183	133	000	038	173	528	Num.Abd.
	000	tr	000	035	025	000	007	033	100	Per Abd.
PT09Ebase bfN PC										
	000	000	000	003	000	000	000	000	3	Num.Abd.
	000	000	000	099	000	000	000	000	99	Per.Abd.
PT09I*l*1/3 bfN PC										
	000	000	000	002	000	000	000	002	4	Num.Abd.
	000	000	000	050	000	000	000	050	100	Per.Abd.
PT09Im1/3 bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT09K*l*1/3 bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT12B*l*1/2 bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT12Bu1/2 bfN PC										
	000	000	000	000	000	000	000	001	1	Num.Abd.
	000	000	000	000	000	000	000	099	99	Per.Abd.
PT12D bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT13Da bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT13Dd bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.

	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
PT13De bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT15C*l*1/3 bfN PC										
	000	000	000	004	051	000	000	009	64	Num.Abd.
	000	000	000	006	080	000	000	014	100	Per.Abd.
PT15Cm1/3 bfN PR										
	000	000	000	026	109	000	000	001	136	Num.Abd.
	000	000	000	019	080	000	000	tr	99	Per.Abd.
PT15Cu1/3 bfN PC										
	000	001	000	077	042	000	008	083	211	Num.Abd.
	000	tr	000	037	020	000	004	039	100	Per.Abd.
PT15Ea bfN PC										
	000	000	000	019	001	000	001	018	39	Num.Abd.
	000	000	000	049	002	000	002	046	99	Per.Abd.
PT16(-A) bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
PT16A bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
RY02C*l*1/3 bfN PR										
	000	000	000	000	159	000	000	064	223	Num.Abd.
	000	000	000	000	071	000	000	029	100	Per.Abd.
RY02Cm1/3 bfN PR										
	000	000	000	024	009	000	000	000	33	Num.Abd.
	000	000	000	073	027	000	000	000	100	Per.Abd.
RY02Cm1/3 bfN PR										
	001	000	000	156	156	000	064	118	495	Num.Abd.
	tr	000	000	032	032	000	013	023	100	Per.Abd.
RY02G/H*l*1/3 bfN PR										
	007	004	000	056	036	000	000	071	175	Num.Abd.
	005	003	000	032	020	000	000	040	100	Per.Abd.
RY02G/Hm1/3 bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
RY02G/Hu1/3 bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
RY02Ja bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
RY02Jb bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
RY02K/L bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GE18(1b) bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GE18(1c) bfN PC										
	000	000	000	001	001	000	000	004	6	Num.Abd.
	000	000	000	017	017	000	000	066	100	Per.Abd.
GE18(1d) bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.

	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
GE18(1e) bfN PC										
	000	000	000	000	000	000	000	000	0	Num. Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GE18(1f) bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GE18(3)*l*1/3 bfN PR										
	000	006	000	063	047	000	000	018	134	Num.Abd.
	000	004	000	047	035	000	000	013	99	Per.Abd.
GE18(3)m1/3 bfN PR										
	000	000	000	006	312	000	000	031	349	Num.Abd.
	000	000	000	002	089	000	000	009	100	Per.Abd.
GE18(3)u1/3 bfN PR										
	002	000	000	093	097	000	032	121	345	Num.Abd.
	001	000	000	027	028	000	009	035	100	Per.Abd.
GE18(5) bfN PR										
	000	000	000	056	031	000	001	051	139	Num.Abd.
	000	000	000	040	022	000	001	037	100	Per.Abd.
GE18(8)*l*1/3 bfN PR										
	000	008	000	042	007	004	000	015	77	Num.Abd.
	000	010	000	055	009	005	000	020	99	Per.Abd.
GE18(8)m1/3 bfN PR										
	000	001	000	017	004	000	000	041	63	Num.Abd.
	000	001	000	027	006	000	000	065	99	Per.Abd.
GE18(8)u1/3 bfN PR										
	002	000	000	000	000	000	000	004	6	Num.Abd.
	033	000	000	000	000	000	000	067	100	Per.Abd.
GE18(10) bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GE18(12) bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GE18(14)*l*1/3 bfN PR										
	000	000	000	010	001	000	000	003	14	Num.Abd.
	000	000	000	071	007	000	000	021	99	Per.Abd.
GE18(14)m1/3 bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GE18(14)u1/3 bfN PR										
	000	004	000	007	046	003	005	052	116	Num.Abd.
	000	003	000	006	040	003	004	045	101	Per.Abd.
GE18(17)*l*1/2 bfN PR										
	000	000	000	002	000	000	000	001	3	Num.Abd.
	000	000	000	066	000	000	000	034	100	Per.Abd.
GE18(17u1/2 bfN PR										
	000	000	000	026	007	000	004	025	62	Num.Abd.
	000	000	000	042	011	000	006	040	99	Per.Abd.
GE18(19) bfN PR										
	000	000	000	000	004	000	000	000	4	Num.Abd.
	000	000	000	000	099	000	000	000	99	Per.Abd.
GE18(21a) bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GE18(21c) bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.

	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
GE18JUL/(21d) bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
WA03G bfN PC										
	000	000	000	000	005	000	000	000	5	Num.Abd.
	000	000	000	000	099	000	000	000	99	Per.Abd.
WA04A bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
WA04I bfN PR										
	002	000	000	018	043	000	002	053	118	Num.Abd.
	001	000	000	015	036	000	001	045	98	Per.Abd.
WA04J bfN PR										
	000	000	000	007	020	000	001	024	52	Num.Abd.
	000	000	000	014	038	000	002	046	100	Per.Abd.
WA04L bfN PR										
	000	000	000	002	012	000	002	014	30	Num.Abd.
	000	000	000	007	040	000	007	046	100	Per.Abd.
WA08Bd bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
WA08Be*l*1/2 bfN PC										
	000	000	000	000	000	000	000	004	4	Num.Abd.
	000	000	000	000	000	000	000	099	99	Per.Abd.
WA08Beu1/2 bfN PC										
	000	000	000	003	003	000	000	010	16	Num.Abd.
	000	000	000	019	019	000	000	062	100	Per.Abd.
WA08D*l*1/3 bfN PR										
	000	000	000	000	110	000	000	024	134	Num.Abd.
	000	000	000	000	082	000	000	018	100	Per.Abd.
WA08Dm1/3 bfN PR										
	000	000	000	021	060	000	000	003	84	Num.Abd.
	000	000	000	025	071	000	000	004	100	Per.Abd.
WA08Du1/3 bfN PC										
	000	001	000	133	168	001	084	254	631	Num.Abd.
	000	tr	000	021	027	tr	013	040	101	Per.Abd.
WA08JUL/F bfN PC										
	000	000	000	038	033	000	000	077	148	Num.Abd.
	000	000	000	026	022	000	000	052	100	Per.Abd.
MS06E*l*1/3 bfN PC										
	000	000	000	013	006	000	000	028	47	Num.Abd.
	000	000	000	028	013	000	000	059	100	Per.Abd.
MS06Em1/3 bfN PC										
	000	001	001	084	041	001	000	056	184	Num.Abd.
	000	tr	tr	046	022	tr	000	030	99	Per.Abd.
MS06Eu1/3 bfN PC										
	000	009	000	043	021	000	016	191	280	Num.Abd.
	000	003	000	015	007	000	006	068	99	Per.Abd.
MS06G bfN PC										
	000	000	000	008	000	000	004	010	22	Num.Abd.
	000	000	000	036	000	000	018	046	100	Per.Abd.
MS21E bfN PC										
	000	000	000	003	004	000	001	004	12	Num.Abd.
	000	000	000	025	033	000	009	033	100	Per.Abd.
MS24A bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.

	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
MS25JUL/B bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
LY02Ad bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
LY02Ae bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
LY02Af bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
LY02C/1/2 bfN PR										
	000	000	000	009	158	000	006	007	180	Num.Abd.
	000	000	000	005	088	000	003	004	100	Per.Abd.
LY02Cu1/2 bfN PR										
	000	002	000	163	042	000	002	034	243	Num.Abd.
	000	001	000	067	017	000	001	014	100	Per.Abd.
LY08JUL/Fb bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH04A bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH04B bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH04C bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH04E/1/2 bfN PR										
	000	000	000	000	025	000	001	001	27	Num.Abd.
	000	000	000	000	093	000	003	003	99	Per.Abd.
CH04Eu1/2 bfN PR										
	000	000	000	031	065	000	005	058	159	Num.Abd.
	000	000	000	019	041	000	003	036	99	Per.Abd.
CH04G bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH05Ba/1/3 bfN PR										
	000	002	000	025	000	000	001	076	104	Num.Abd.
	000	002	000	024	000	000	001	073	100	Per.Abd.
CH05Bam1/3 bfN PR										
	000	000	000	000	003	000	000	033	36	Num.Abd.
	000	000	000	000	008	000	000	092	100	Per.Abd.
CH05Bau1/3 bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH05Bc bfN PR										
	000	000	000	000	000	000	000	015	15	Num.Abd.
	000	000	000	000	000	000	000	099	99	Per.Abd.
CH16B bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH16C bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.

	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
CH16D bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH16F*l*1/3 bfN PR										
	000	000	000	041	020	000	003	003	67	Num.Abd.
	000	000	000	061	030	000	004	004	99	Per.Abd.
CH16Fm1/3 bfN PR										
	000	002	000	024	050	000	001	060	137	Num.Abd.
	000	001	000	013	041	000	001	044	100	Per.Abd.
CH16Fu1/3 bfN PR										
	000	004	000	036	060	000	001	071	172	Num.Abd.
	000	002	000	021	035	000	tr	041	100	Per.Abd.
CH16H bfN PC										
	000	000	000	000	000	000	003	020	23	Num.Abd.
	000	000	000	000	000	000	013	087	100	Per.Abd.
CH22Cam1/3 bfN PC										
	000	000	000	039	015	000	004	068	126	Num.Abd.
	000	000	000	031	012	000	003	054	100	Per.Abd.
CH35N bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH35O bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH39Ab bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH39Ac bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH39Ad bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH44B*l*1/2 bfN PC										
	000	000	000	006	007	000	000	014	27	Num.Abd.
	000	000	000	022	026	000	000	052	100	Per.Abd.
CH44Bu1/2 bfN PC										
	000	000	000	000	000	000	000	004	4	Num.Abd.
	000	000	000	000	000	000	000	099	99	Per.Abd.
CH45(-A)*l*1/3 bfN PR										
	000	007	001	020	019	000	001	059	107	Num.Abd.
	000	007	001	019	017	000	001	055	100	Per.Abd.
CH45(-A)*l*/m1/3 bfN PC										
	000	000	000	006	000	000	000	000	6	Num.Abd.
	000	000	000	099	000	000	000	000	99	Per.Abd.
CH45(-A)m1/3 bfN PC										
	000	000	000	003	000	000	000	000	3	Num.Abd.
	000	000	000	099	000	000	000	000	99	Per. Abd.
CH45(-A)u1/3 bfN PR										
	000	000	000	018	002	000	000	013	33	Num.Abd.
	000	000	000	055	005	000	000	040	100	Per.Abd.
CH45B bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CH45D*l*1/2 bfN PC										
	000	000	000	000	010	000	007	004	21	Num.Abd.
	000	000	000	000	048	000	033	019	100	Per.Abd.

	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
CH45Du1/2 bfN PC										
	000	000	000	001	005	000	008	004	18	Num.Abd.
	000	000	000	005	027	000	045	023	100	Per.Abd.
CH48JUL/A bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GR01Aa bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GR01Ab bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GR01Ac bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GR01Ad-e bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GR01C bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GR01D bfN PC										
	000	000	000	031	024	000	000	000	55	Num.Abd.
	000	000	000	056	043	000	000	000	99	Per.Abd.
GR01E*l*1/3 bfN PR										
	000	000	000	031	016	000	000	010	57	Num.Abd.
	000	000	000	054	028	000	000	018	100	Per.Abd.
GR01Em1/3 bfN PR										
	000	000	000	021	005	000	000	014	40	Num.Abd.
	000	000	000	052	012	000	000	035	99	Per.Abd.
GR01Eu1/3 bfN PR										
	000	000	000	041	033	000	000	003	77	Num.Abd.
	000	000	000	053	043	000	000	004	100	Per.Abd.
GR01I bfN PR										
	000	004	000	052	008	001	000	015	80	Num.Abd.
	000	005	000	065	010	001	000	019	100	Per.Abd.
GR01J*l*1/2 bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GR01Ju1/2 bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GR01K bfN PC										
	000	001	000	001	000	000	000	000	2	Num.Abd.
	000	050	000	050	000	000	000	000	100	Per.Abd.
GR01L*l*1/3 bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
GR01Lm1/3 bfN PC										
	000	000	000	026	000	000	000	000	26	Num.Abd.
	000	000	000	099	000	000	000	000	99	Per.Abd.
GR01JUL/Lu1/3 bfN PC										
	000	000	000	000	001	000	003	011	15	Num.Abd.
	000	000	000	000	007	000	020	073	100	Per.Abd.
BU04Aa bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.

ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
BU04Bbase bfN PC									
000	000	000	001	000	000	001	001	3	Num.Abd.
000	000	000	033	000	000	033	033	99	Per.Abd.
BU04Ju1/2 bfN PR									
000	000	000	025	004	000	006	013	48	Num.Abd.
000	000	000	052	008	000	012	027	99	Per.Abd.
BU04L*l*1/3 bfN PC									
000	000	000	000	001	000	000	001	2	Num.Abd.
000	000	000	000	050	000	000	050	100	Per.Abd.
BU04Lm1/3 bfN PC									
000	000	000	026	000	000	007	000	33	Num.Abd.
000	000	000	078	000	000	021	000	99	Per.Abd.
BU04Lu1/3 bfN PR									
000	000	000	048	004	000	000	017	69	Num.Abd.
000	000	000	070	006	000	000	024	100	Per.Abd.
BU04N*l*1/2 bfN PC									
000	000	000	010	000	000	000	004	14	Num.Abd.
000	000	000	071	000	000	000	029	100	Per.Abd.
BU04Nu1/2 bfN PR									
000	011	000	042	026	001	004	037	121	Num.Abd.
000	009	000	035	022	tr	003	030	99	Per.Abd.
BU04P*l*1/3 bfN PR									
000	001	000	011	009	000	003	005	29	Num.Abd.
000	004	000	038	031	000	010	017	100	Per.Abd.
BU04Pm1/3 bfN PR									
000	001	000	008	009	000	021	022	61	Num.Abd.
000	002	000	013	015	000	034	036	100	Per.Abd.
BU04Pu1/3 bfN PR									
000	003	000	023	020	001	015	047	109	Num.Abd.
000	003	000	021	018	001	014	043	100	Per.Abd.
BU04R bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
BU04S bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
BU05G bfN PR									
000	000	000	042	000	000	000	003	45	Num.Abd.
000	000	000	093	000	000	000	007	100	Per.Abd.
BU05I*l*1/2 bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
BU05JUL/1u1/2 bfN PC									
000	000	000	000	001	001	000	003	5	Num.Abd.
000	000	000	000	020	020	000	060	100	Per.Abd.
CY09(-B) bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
CY09Aa bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
CY09Ab bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
CY15(1b) bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.

	ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
CY15(1c) bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY15B bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY15G bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY30Am1/3 bfN PC										
	000	000	000	000	006	000	000	000	6	Num.Abd.
	000	000	000	000	099	000	000	000	99	Per.Abd.
CY30Au1/3 bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY30Bm1/3 bfN PR										
	000	000	000	006	000	000	000	026	32	Num.Abd.
	000	000	000	019	000	000	000	081	100	Per.Abd.
CY30G bfN PC										
	000	000	000	000	000	000	000	005	5	Num.Abd.
	000	000	000	000	000	000	000	099	99	Per.Abd.
CY32Ac bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY32C bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY32Hb bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY32Hc bfN PC										
	000	000	000	000	001	000	000	001	2	Num.Abd.
	000	000	000	000	050	000	000	050	100	Per.Abd.
CY42A bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY42Bbase bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY42Bu1/2 bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY42C bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY42E bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY42G bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY43A bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.
CY43Bl1/3 bfN PC										
	000	000	000	000	000	000	000	000	0	Num.Abd.
	000	000	000	000	000	000	000	000	0	Per.Abd.

ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
CY43Bm1/3 bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
CY43JUL/Bu1/3 bfN PC									
000	000	000	018	000	000	000	002	20	Num.Abd.
000	000	000	090	000	000	000	010	100	Per.Abd.
KA01B bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
KA01L*l*1/2 bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
KA02E bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
KA02Fb bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
KA02I*l*1/2 bfN PC									
000	000	000	014	001	000	000	014	29	Num.Abd.
000	000	000	048	004	000	000	048	100	Per.Abd.
KA02Iu1/2 bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
KA02Ka bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
KA02L bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
KA04A bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
KA04C bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
KA05E bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
KA05F bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
KA05I*l*1/2 bfN PC									
000	000	000	021	000	000	000	000	21	Num.Abd.
000	000	000	099	000	000	000	000	99	Per.Abd.
KA05Iu1/2 bfN PC									
000	000	000	007	000	000	000	000	7	Num.Abd.
000	000	000	099	000	000	000	000	99	Per.Abd.
KA05JUL/N bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
OS01(-B) bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
OS01A bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.

ETL	ESL	BIF	DBR	RPI	RBR	DPI	FEN	TOTALS	
OS01JUL/C/1/3 bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.
PW01JUL/A bfN PC									
000	000	000	000	000	000	000	000	0	Num.Abd.
000	000	000	000	000	000	000	000	0	Per.Abd.

APPENDIX B—SUMMARY NUMERICAL TABLES

The following set of tables summarizes the numerical data obtained by me through examination of 1,027 specimens of Wreford rhabdomesid cryptostomes. In addition, type specimens of *Rhombopora lepidodendroides* were obtained from the Smithsonian Institution and examined. This collection of eleven slides is discussed elsewhere in the text. Here, their measurements are presented under the heading "Type Suite."

Though 943 of the 1,027 specimens were of *Rhombopora lepidodendroides* MEEK, the total number of measurements for any parameter is always less than 600. The same situation is true for *Syringoclemis wrefordensis;* the total number of measurements is less than the number of specimens. This is because not all parameters were assessable on every specimen.

All computations, as discussed in the text, were performed on the IBM System 360/67 Computer through the use of The Pennsylvania State University Computation Center's library programs. Both STSUM of the STPAC system and NORM were used from this library of programs.

All measurements were made in millimeters and, except for the meristic characters, millimeters are the units for all measurements. The omission of dimensions is only to save space.

Numerical Summary of MWZ (Maximum Width of Zoarium) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	579	1.669	1.30	.67247	.50-4.40
Skewness	**Kurtosis**	**Coefficient of Variation**			
.22271	-.25713	40.3			

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	4	2.60	1.90-3.20

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	77	1.10	1.00	.29761	.50-1.80
Skewness	**Kurtosis**	**Coefficient of Variation**			
.000016	-.16194	27.1			

Numerical Summary of TP (Thickness of the Peripheral Zone) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	567	.385	.260	.1863	.06-1.40
Skewness	**Kurtosis**	**Coefficient of Variation**			
.3876	2.3633	48.4			

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	4	.5525	.30-.60

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	77	.170	.180	.0616	.09-.31
Skewness	**Kurtosis**	**Coefficient of Variation**			
.3367	1.7110	36.3			

Numerical Summary of Z1 (Number of Zooecial Openings in One Square Millimeter) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	533	9.35	10	1.905	5-19

Skewness	Kurtosis	Coefficient of Variation
.23196	.3405	20.4

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	4	10.5	9-12

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	79	14.0	18	7.071	7-32
Skewness	**Kurtosis**	**Coefficient of Variation**			
0.0	-1.00	50.5			

Numerical Summary of Z2 (Number of Zooecial Openings in Two Millimeters Parallel to Zoarial Axis) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	527	5.25	5	1.022	4-9
Skewness	**Kurtosis**	**Coefficient of Variation**			
.94288	2.4571	19.4			

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	6	5.20	5-6

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	77	9.0	9	2.00	5-15
Skewness	**Kurtosis**	**Coefficient of Variation**			
.34694	.23469	22.2			

Numerical Summary of ZA (Number of Zooecial Apertures in Transverse Section) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	558	14.0	13	3.980	7-33
Skewness	**Kurtosis**	**Coefficient of Variation**			
0.1139	-.3615	28.4			

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	4	18.5	15-24

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	76	16.60	20	4.2779	10-23
Skewness	**Kurtosis**	**Coefficient of Variation**			
-.6780	2.1616	25.8			

Numerical Summary of MZAD (Maximum Diameter of Zooecial Aperture) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	578	.260	.250	.0435	.14-.53
Skewness	**Kurtosis**	**Coefficient of Variation**			
1.3885	10.3518	16.7			

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	4	.245	.22-.26

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	76	.180	.180	.0292	.14-.30
Skewness	**Kurtosis**	**Coefficient of Variation**			
.0002	2.2256	16.2			

Numerical Summary of AZD (Average Zooecial Depth) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	524	.996	.70	.3663	.40-3.10
Skewness	**Kurtosis**	**Coefficient of Variation**			
.27810	-.23694	36.8			

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	8	1.55	1.20-1.80

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	77	.6428	.60	.22254	.30-1.90
Skewness	**Kurtosis**	**Coefficient of Variation**			
.051005	-.26596	34.6			

Numerical Summary of IWT (Inter-apertural Wall Thickness) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	563	.123	.120	.0409	.03-.31
Skewness	**Kurtosis**	**Coefficient of Variation**			
.05025	-.15513	33.4			

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	14	.132	.10-.13

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	76	.030	.030	.00820	.02-.11
Skewness	**Kurtosis**	**Coefficient of Variation**			
0.0000	2.0005	27.2			

Numerical Summary of NMSP (Number of Mesopores Encountered in One Square Millimeter) Observations.

Rhombopora lepidodendroides

Statistical summary including zero values:

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	540	.571	0	1.3986	0-16
Skewness	**Kurtosis**	**Coefficient of Variation**	**Percentage without Mesopores**		
1.2809	2.7221	244.8	74.35%		

Statistical summary excluding zero values:

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	139	2.00	2	1.1547	1-16
Skewness	**Kurtosis**	**Coefficient of Variation**			
.35078	-.40625	57.7			

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	4	0.0	0.0-0.0

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	77	37.14	44	13.704	8-67
Skewness	**Kurtosis**	**Coefficient of Variation**			
.78231	.55136	36.9			

Numerical Summary of MMSP (Maximum Mesopore Width as Measured in Tangential Section) Observations.

Rhombopora lepidodendroides

Statistical summary including zero values:

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	548	.025	0.0	.0447	0.0-.21
Skewness	**Kurtosis**	**Coefficient of Variation**			
.72830	.36963	177.5			

Statistical summary excluding zero values:

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	133	.0875	.080	.0296	.03-.21
Skewness	**Kurtosis**	**Coefficient of Variation**			
.046178	-.043489	33.9			

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	20	0.0	0.0-0.0

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	76	.074	.080	.02408	.04-.11
Skewness	**Kurtosis**	**Coefficient of Variation**			
.20170	-.61823	32.5			

Numerical Summary of NMA (Number of Megacanthopores in One Square Millimeter in Tangential Section) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	526	11.70	12	3.0736	1.0-22.0
Skewness	**Kurtosis**	**Coefficient of Variation**			
.62289	1.9844	26.3			

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	5	11.5	10-13

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	77	37.25	42	14.17	17-111

Skewness	Kurtosis	Coefficient of Variation
.41243	-.52574	38.1

Numerical Summary of MMAW (Maximum Megacanthopore Width Observed in Tangential Section) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	564	.085	.080	.0234	.03-.17

Skewness	Kurtosis	Coefficient of Variation
.06234	-.02048	27.5

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	24	.095	.06-.12

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	77	.035	.040	.0100	.02-.06

Skewness	Kurtosis	Coefficient of Variation
.57735	-.33338	28.6

Numerical Summary of NRIW (Number of Micracanthopors Rows Observed in the Interapertural Space in Tangential Section) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	531	2.077	2	.74421	1.0-4.0

Skewness	Kurtosis	Coefficient of Variation
.23717	.12963	35.8

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	4	2.75	2-3

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	79	0.0	0.0	0.0	0.0

Skewness	Kurtosis	Coefficient of Variation
00.00	00.00	0.0

Numerical Summary of NMU (Number of Micracanthopores in One Square Millimeter) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	524	41.28	36	11.477	11-72

Skewness	Kurtosis	Coefficient of Variation
.63341	1.4756	27.8

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	5	55.25	46-65

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	79	0.0	0.0	0.0	0.0-0.0

Skewness	Kurtosis	Coefficient of Variation
00.00	00.00	00.

Numerical Summary of MNUW (Maximum Number of Micracanthopores Observed Between Two Megacanthopores in Tangential Section) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	528	4.11	4	1.013	1-7

Skewness	Kurtosis	Coefficient of Variation
.33821	.94875	24.6

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	4	5.50	5.0-6.0

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	79	0.0	0.0	0.0	0.0

Skewness	Kurtosis	Coefficient of Variation
00.00	00.00	0.0

Numerical Summary of MMUW (Maximum Micracanthopores Width Observed in Tangential Section) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	574	.045	.045	.0106	.02-.08
Skewness	Kurtosis	Coefficient of Variation			
.16675	-.18705	23.8			

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	4	.0375	.03-.04

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	79	0.0	0.0	0.0	0.0-0.0
Skewness	Kurtosis	Coefficient of Variation			
00.00	00.00	0.0			

Numerical Summary of DTZ_2 (Number of Diaphragms Encountered in Two Millimeters Parallel to Zoarial Axis) Observations.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
943	543	1.89	0.00	2.685	0.0-15
Skewness	Kurtosis	Coefficient of Variation			
.69508	.60830	141.9			

Type Suite

Number of Specimens	Number of Measures	Median	Range of Observations
4	8	2.0	1-5

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Mean	Mode	Standard Deviation	Range of Observations
84	76	.375	0.00	1.060	0.0-7
Skewness	Kurtosis	Coefficient of Variation			
1.1339	1.5714	282.8			

Numerical Summary of NIHS (Number of Possible Inferior Hemisepta) and NSHS (Number of Possible Superior Hemisepta) for Syringoclemis wrefordensis, *the Type Suite, and* Rhombopora lepidodendroides *Combined.*

Number of Measures	Number of Specimens	Number of Zero Counts (Total)	Mean	Mode	Standard Deviation
1217	943	1201	0.00	0.00	0.00
Skewness	Kurtosis	Coefficient of Variation	Percentage of Total = Zero		
46×10^{62}	29×10^{-78}	0.0	98.9%		

Numerical Summary of Percent of Specimens Possessing the Basal Lamina.

Rhombopora lepidodendroides

Number of Specimens	Number of Measures	Number with Lamina	Percentage with Lamina
943	568	48	0.844%

Type Suite

Number of Specimens	Number of Measures	Number with Lamina	Percentage with Lamina
4	4	0.0	0.00%

Syringoclemis wrefordensis

Number of Specimens	Number of Measures	Number with Lamina	Percentage with Lamina
84	77	30	38.99%

APPENDIX C—GENERA AND SPECIES OF THE FAMILY RHABDOMESIDAE

Listed for each genus of the family Rhabdomesidae are its name, author, and date, followed below by its type-species as currently designated and then as it was originally designated. Following this, all species in each genus are listed, along with their geologic and geographic positions from which they were originally described. The genera are listed alphabetically. The species within each genus are also listed alphabetically.

ACANTHOCLEMA Hall, 1886
A. alternata (Hall, 1883), as *Trematopora alternata*
A. alternata (Hall), Middle Devonian (Onondag.), New York
A. asperum (Hall), Silurian (Rochester), New York, Ontario
A. confluens (Ulrich), Mississippian (Keokuk), Iowa
A. divergens Hall & Simpson, Devonian (Helderberg.), New York
A. lineatum McNair, Devonian (Traverse), Michigan
A. ohioense McNair, Devonian (Traverse), Ohio
A. sulcatum Hall & Simpson, Devonian (Hamilton), New York
A. triseriale (Hall), Devonian (Helderberg.), New York

ASCOPORA Trautschold, 1876
A. rhombifera (Phillips, 1836), as *Millepora rhombifera*
A. asiatica Sakagami, Permian, Thailand
A. magma Sakagami, Permian, Thailand
A. nakornsrii Sakagami, Permian, Thailand
A. rhombifera (Phillips), Lower Carboniferous, England
A. yanagidae Sakagami, Permian, Thailand

BACTROPORA Hall & Simpson, 1887
B. granistriata (Hall, 1883), as *Trematopora granistriata*
B. curvata Hall & Simpson, Devonian (Hamilton), New York
B. granistriata (Hall), Devonian (Hamilton), New York
B. simplex Ulrich, Mississippian (Keokuk), Iowa

CLAUSOTRYPA Bassler, 1929
C. separata Bassler, 1929

C. exillis SAKAGAMI, Permian *(Lepidolina-Yabeina)*, Japan
C. minor BASSLER, Permian, Timor
C. separata BASSLER, Permian, Timor

COELOCONUS ULRICH, 1889
C. rhombicus ULRICH, 1889
C. compositus CERETTI, Carboniferous, Carnic Alps, Italy
C. granosus ULRICH, Mississippian (Chester.), Illinois
C. hirtus CERETTI, Carboniferous, Carnic Alps, Italy
C. rhombicus ULRICH, Mississippian (Warsaw), Illinois
C. tuba GIRTY, Mississippian (Chester.), Arkansas

GOLDFUSSITRYPA BASSLER, 1952
G. estonia (BASSLER, 1911), as *Rhombopora esthonia*
G. estonia (BASSLER), Middle Ordovician, Esthonia

HAYASAKAPORA SAKAGAMI, 1960
H. erectoradiata SAKAGAMI, 1960
H. erectoradiata SAKAGAMI, Permian, Japan
H. matsudae SAKAGAMI, Permian *(Parafusulina)*, Japan
H. taishakuensis SAKAGAMI, Permian *(Pseudoschwagerina)*, Japan

HYALOTOECHUS MCNAIR, 1942
H. duncani MCNAIR, 1942
H. duncani MCNAIR, Devonian (Chemung), New York
H. subannulata (ULRICH), Middle Devonian, Iowa

HYPHASMOPORA ETHERIDGE, 1875
H. buskii ETHERIDGE, 1875
H. buskii ETHERIDGE, Lower Carboniferous, Scotland

IDIOCLEMA GIRTY, 1911
I. insigne GIRTY, 1911
I. insigne GIRTY, Mississippian (Chester.), Arkansas

LINOTAXIS BASSLER, 1952
L. magna (MCNAIR, 1942), as *Orthopora magna*
L. magna (MCNAIR), Devonian (Chemung), New York

MEGACANTHOPORA MOORE, 1929
M. fallacis MOORE, 1929
M. fallacis MOORE, Upper Pennsylvanian (Graham), Texas

NEMATAXIDRA BASSLER, 1952
N. piercensis BASSLER, 1952
N. piercensis BASSLER, Ordovician (Blackriver), Tennessee

NEMATAXIS HALL, 1886
N. fibrosus HALL, 1886
N. fibrosus HALL, Middle Devonian (Onondag.), Ontario
N. simplex HALL & SIMPSON, Devonian (Hamilton), New York

NEMATOTRYPA BASSLER, 1911
N. gracilis BASSLER, 1911
N. gracilis BASSLER, Ordovician, Esthonia

NICKLESOPORA BASSLER, 1952
N. elegantula (ULRICH, 1884), as *Rhombopora elegantula*
N. elegantula (ULRICH), Lower Mississippian (Osag.), Kentucky

ORTHOPORA HALL, 1886
O. regularis (HALL, 1874) as *Trematopora regularis*
O. acuta MCNAIR, Devonian (Chemung), New York
O. bispinulata (HALL), Devonian (Hamilton), New York
O. bucheri FENTON & FENTON, Devonian (Hackberry), Iowa
O. canaliculata (HALL), Devonian (Helderberg.), New York
O. carinata (HALL & SIMPSON), Devonian (Hamilton), New York
O. elongata (HALL & SIMPSON), Devonian (Hamilton), New York
O. granifera (HALL & SIMPSON), Devonian (Hamilton), New York
O. granilinea (HALL & SIMPSON), Devonian (Helderberg.), New York
O. hexagona (HALL & SIMPSON), Devonian (Hamilton), New York
O. immersa (HALL & SIMPSON), Devonian (Hamilton), New York
O. interplana (HALL & SIMPSON), Devonian (Hamilton), New York
O. lineata (HALL & SIMPSON), Devonian (Hamilton), New York
O. magna MCNAIR, Devonian (Chemung), New York
O. nodosa (HALL & SIMPSON), Devonian (Helderberg.), New York
O. orbipora (HALL), Devonian (Hamilton), New York
O. ornata (HALL & SIMPSON), Devonian (Hamilton), New York
O. ovatipora (HALL), Devonian (Helderberg.), New York
O. parallela (HALL), Devonian (Helderberg.), New York
O. polygona (HALL), Devonian (Helderberg.), New York
O. regularis (HALL), Devonian (Helderberg.), New York
O. reticulata (HALL & SIMPSON), Devonian (Hamilton), New York
O. rhombifera (HALL), Devonian, West Virginia
O. scutulata (HALL), Devonian (Helderberg.), New York
O. subquadrata (HALL & SIMPSON), Devonian (Hamilton), New York
O. tortalinea (HALL), Devonian (Hamilton), New York

OTTOSEETAXIS BASSLER, 1952
O. bipartitus BASSLER, 1952
O. bipartitus BASSLER, Ordovician (Blackriver), Tennessee

PETALOPORELLA PRANTL, 1935
P. bohemica PRANTL, 1935
P. bohemica PRANTL, Devonian, Czechoslovakia

RHABDOMESON YOUNG & YOUNG, 1874
R. gracile (PHILLIPS, 1841), as *Millepora gracilis*
R. bellum MOORE, Upper Pennsylvanian (Graham), Texas
R. bispinosa CROCKFORD, Lower Permian (Callytharra), Australia
R. consimile BASSLER, Upper Permian, Timor
R. (Rhombopora) foerstei ELIAS, Pennsylvanian, Oklahoma
R. gracile (PHILLIPS), Lower Carboniferous, England
R. mammillatum (BRETNALL), Permian (Lower?), W. Australia
R. nakazawae SAKAGAMI, Lower Permian, Japan
R. ofukuensis SAKAGAMI, Permian, Japan
R. propatulissiumum CERETTI, Carboniferous, Carnic Alps, Italy
R. rhombiferum (PHILLIPS), Lower Carboniferous, England
R. (Rhombopora) rogersi ELIAS, Pennsylvanian, Oklahoma
R. spinosum MOROZOVA, Lower Carboniferous, Don Valley, USSR
R. (Rhombopora) ulrichi ELIAS, Pennsylvanian, Oklahoma
R. yabei SAKAGAMI, Lower Carboniferous, Japan

RHOMBOCLADIA ROGERS, 1900
R. delicata ROGERS, 1900
R. carnica CERETTI, Upper Carboniferous, Carnic Alps, Italy
R. borissiaki SHULGA-NESTERENKO, Lower Carboniferous, Russian Platform
R. coronata SHULGA-NESTERENKO, Middle Carboniferous, Russian Platform
R. delicata ROGERS, Upper Pennsylvanian (Iola Ls.), Missouri
R. johnseni CERETTI, Upper Carboniferous, Carnic Alps, Italy
R. kasimovensis SHULGA-NESTERENKO, Upper Carboniferous, Russian Platform
R. ninae SHULGA-NESTERENKO, Upper Carboniferous, Russian Platform

R. septata SHULGA-NESTERENKO, Lower Carboniferous, Russian Platform
R. tenuata SHULGA-NESTERENKO, Upper Carboniferous, Russian Platform

RHOMBOPORA MEEK, 1872
R. lepidodendroides MEEK, 1872
R. angustata ULRICH, Mississippian (Keokuk), Kentucky
R. armata ULRICH, Mississippian (Chester.), Illinois
R. asperula ULRICH, Mississippian (Keokuk), Iowa
R. attenuata ULRICH, Mississippian (Keokuk), Iowa
R. bigemmis (KEYSERLING), Carboniferous, India
R. constans MOORE, Upper Pennsylvanian (Graham), Texas
R. crassa ULRICH, Pennsylvanian, Missouri
R. decipiens ULRICH, Mississippian (Saint Louis), Illinois
R. dichotoma ULRICH, Mississippian (Keokuk), Illinois
R. elegantula ULRICH, Mississippian (Keokuk), Kentucky
R. exigua ULRICH, Mississippian (Burlington), Iowa, Japan
R. exillis (DAWSON), Carboniferous, Nova Scotia
R. gracilis ULRICH, Mississippian (Burlington), Iowa
R. gratiosa BASSLER, Upper Permian, Timor
R. incrassata ULRICH, Mississippian (Keokuk), Kentucky
R. lepida NIKIFOROVA, Upper Carboniferous, Baskirian Urals, USSR
R. lepidodendroides MEEK, Upper Pennsylvanian, Nebraska
R. lineinodis ULRICH, Devonian (Hamilton), Kentucky
R. mawi OWEN, SILURIAN (Wenlock), England
R. mesopora OWEN, Silurian (Ludlow), England
R. millepuncta MCFARLAN, Mississippian (Chester.), Illinois
R. minima OWEN, Silurian (Ludlow), England
R. minor ULRICH, Mississippian (Chester.), Illinois, Kentucky
R. monogemmis TOULA, Carboniferous, Barents Islands
R. multipora FOERSTE, Pennsylvanian (Pottsville), Ohio
R. munda MOORE, Upper Pennsylvanian (Graham), Texas
R. nicklesi ULRICH, Lower Pennsylvanian, Ohio
R. nova CERETTI, Upper Carboniferous, Italy
R. obliqua WAAGEN, Permian, India (Salt Range)
R. ohioensis ULRICH, Mississippian (Waverly), Ohio
R. orientalis BASSLER, Upper Permian, Timor
R. persimilis ULRICH, Mississippian (Chester.), Illinois, Kentucky
R. picchuensis CHRONIC, Lower Permian, Peru
R. polyporata WAAGEN, Permian, India (Salt Range)
R. porifera FRITZ, Permian, Vancouver, B.C., Canada
R. pulchella ULRICH, Mississippian (Chester.), Illinois, Kentucky
R. pulchra BASSLER, Upper Permian, Timor
R. radialis OWEN, Lower Carboniferous (Visean), England
R. schellwieni JOHNSON, Upper Carboniferous, Carnic Alps, Italy
R. simulatrix ULRICH, Mississippian (Saint Louis), Illinois
R. spiralis ULRICH, Mississippian (Keokuk), Kentucky
R. subannulata ULRICH, Devonian (Hamilton), New York
R. sulcifera ULRICH, Devonian (Hamilton), Iowa
R. tabulata ULRICH, Mississippian (Chester.), Illinois, Kentucky
R. tenuirama ULRICH, Mississippian (Chester.), Illinois, Kentucky
R. tenuis HINDE, Carboniferous (?), W. Australia
R. transversalis ULRICH, Mississippian (Keokuk), Illinois
R. varia ULRICH, Mississippian (Keokuk), Illinois
R. wanneri BASSLER, Upper Permian, Timor
R. wortheni ULRICH, Mississippian (Saint Louis), Kentucky

RHOMBOPORELLA BASSLER, 1936
R. typica BASSLER, 1936
R. typica BASSLER, Carboniferous, Bolivia

SAFFORDOTAXIS BASSLER, 1952
S. incrassata (ULRICH, 1888), as *Rhombopora incrassata*
S. elegans CROCKFORD, Permian (Artinsk.), W. Australia
S. incrassata (ULRICH), Lower Mississippian (Osag.), Kentucky
S. morikawae SAKAGAMI, Permian *(Parafusulina)*, Japan
S. multigranulata (BRETNALL), Permian (Artinsk.), W. Australia
S. multinodata WASS, Permian (Kazan.), Queensland, Australia
S. wanneri (BASSLER), Permian, Timor
S. yanagidae SAKAGAMI, Lower Carboniferous, Japan

SPIRILLOPORA GUERICH, 1896
S. anguillata GUERICH, 1896
S. anguillata GUERICH, Lower Devonian, Poland

STREBLASCOPORA BASSLER, 1952
S. fasciculata (BASSLER, 1929), as *Streblotrypa fasciculata*
S. amabilis SAKAGAMI, Lower Carboniferous, Japan
S. antiqua SAKAGAMI, Lower Carboniferous, Japan
S. biserialis (BASSLER), Permian, Timor
S. browni (ETHERIDGE), Permian, Port Keats, Australia
S. cyclocentrica (TRIZNA), Lower Carboniferous (Visean), USSR
S. delicatula SAKAGAMI, Permian *(Parafusulina)*, Japan
S. dense (MOROZOVA), Permian (Gzhelian), Don Valley, USSR
S. diaphragma SAKAGAMI, Permian, Japan
S. etheridgei (BRETNALL), Permian, Port Keats, Australia
S. fasciculata (BASSLER), Permian, Timor
S. germana (BASSLER), Permian, Timor
S. lineata SAKAGAMI & AKAGI, Lower Permian, S.W. Japan
S. marmionensis (BRETNALL), Permian, Port Keats, Australia
S. nikiforovae (MOROZOVA), Permian (Gzhel.), Don Valley, USSR
S. pulchra (FRITZ), Permian, Vancouver, British Columbia
S. ratburiensis SAKAGAMI, Permian, Thailand
S. supergrossa SAKAGAMI, Lower Permian, Japan
S. tenuis BARANOVA, Lower Carboniferous, USSR

STREBLOCLADIA CROCKFORD, 1944
S. excavata CROCKFORD, 1944
S. excavata CROCKFORD, Permian, W. Australia

STREBLOTRYPA VINE, 1885
S. nicklesi VINE, 1885
S. amplexa ULRICH, Mississippian (Waverly), Ohio
S. anomola MCNAIR, Devonian (Traverse), Ohio
S. cortacea OWEN, Lower Carboniferous (Visean), England
S.? crassa SAKAGAMI, Permian, Thailand
S. (Leioclema?) denticulata ULRICH, Mississippian (Waverly), Ohio
S. distincta ULRICH, Mississippian (Chester.), Illinois
S. germana BASSLER, Upper Permian, Timor
S. hamiltonensis (NICHOLSON), Devonian (Hamilton), Ontario
S. hertzeri ULRICH, Mississippian (Keokuk), Illinois
S. malefistulosa CERETTI, Carboniferous, Carnic Alps, Italy
S. merceri MORNINGSTAR, Pennsylvanian (Pottsville), Ohio
S. multiporata ULRICH, Mississippian (Waverly), Ohio
S. nicklesi VINE, Upper Mississippian (Chester.), Illinois
S. nicklesi ULRICH, Carboniferous, England (clearly a homonym)
S. obliqua ULRICH, Mississippian (Waverly), Ohio
S. pectinata OWEN, Lower Carboniferous (Visean), England
S. prisca (GABB & HORN), Mississippian/Pennsylvanian?, Texas
S. radialis ULRICH, Mississippian (Keokuk), Illinois
S. rarefistulosa CERETTI, Carboniferous, Carnic Alps, Italy
S. regularis ULRICH, Mississippian (Waverly), Ohio
S. scutulata (HALL), Devonian (Hamilton), New York

S. spinifera CERETTI, Carboniferous, Carnic Alps, Italy
S. striata ULRICH, Mississippian (Waverly), Ohio
S. striatopora ROGERS, Carboniferous, Kansas
S. subspinosa ULRICH, Mississippian (Chester.), Illinois
S. ulrichi ROGERS, Pennsylvanian (Iola Fm.), Missouri
S. vulgaris SHULGA-NESTERENKO, Lower Permian, Central Urals
S. sp. CHRONIC, Middle Pennsylvanian (Tarma Gr.), Peru

STREBLOTRYPELLA NIKIFOROVA, 1948
S. major (ULRICH, 1889), as *Streblotrypa major*
S. amicula SAKAGAMI, Lower Carboniferous, Japan
S. astrovae SAKAGAMI, Lower Carboniferous, Japan
S. major (ULRICH), Mississippian (Keokuk), Iowa
S. parallela (CROCKFORD), Lower Carboniferous, New South Wales
S. variopitata TRIZNA, Lower Visean, Kuznetsk Basin, USSR

SYRINGOCLEMIS GIRTY, 1911
S. biserialis GIRTY, 1911
S. biserialis GIRTY, Upper Mississippian (Chester.), Arkansas
S. wrefordensis NEWTON, Lower Permian (Wreford Megacyclothem), Kansas

TROPIDOPORA HALL, 1886
T. nana HALL, 1886
T. nana HALL, Devonian (Helderberg./Onondag.), New York

EXPLANATION OF PLATES

PLATE 1

(All figures are ×45, unless otherwise indicated.)

FIGURE

1-6, 11, 12. *Rhombopora lepidodendroides* MEEK.
1, Scanning electron microscope photograph (×75) of CH09I (float)-p-PC-6101, showing external arrangement of acanthopores; 2-4, transverse, tangential, and longitudinal section of PT15C(u 1/3)-bfN-PC-6102, illustrating near identity in micracanthopores and megacanthopores; 5, tangential section of GE18(8) (m 1/3) (float)-p-PC-6101 showing the approximate identity of the size of megacanthopores and micracanthopores; 6, longitudinal section of PT16D (float)-p-PC-6101; 11, longitudinal section of RY02C(m 1/3)-bfN-6101, showing nearly replaced brachiopod spine and basal lamina (epitheca) development; 12, longitudinal section of CH04E-bfN-PR-6101, showing completed removal of central brachiopod (small echinoid?) spine and its replacement by clear, sparry calcite.

7-10, 13-15. *Syringoclemis wrefordensis* NEWTON, n. sp. 7, longitudinal section of the holotype, CY15(4) (float)-p-PC-1601, a typical solid-ramose specimen; 8, tangential section of the holotype, showing typical arrangement of mesopores and acanthopores; 9, transverse section of paratype GE18(19)-bfN-PR6101, showing hollow axial portion (site of exsolved cylindrical element); 10, longitudinal section of paratype WA08Be(u 1/2)-bfN-PC-6101, showing a wholly intact brachiopod spine in center and basal lamina overgrowth; 13, longitudinal section of paratype PT15C (u 1/3)-bfN-PC-6102, showing another brachiopod spine as center axis; 14, longitudinal section of paratype GE18(19)-bfN-PR-6101, showing complete removal of central body and its replacement by limonitic(?) micrite; 15, same view as in Figure 14, only ×27.

PLATE 2

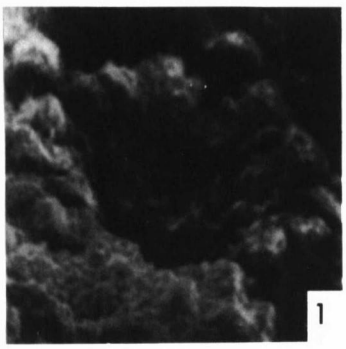
(All figures are ×45, unless otherwise indicated.)

FIGURE

1-8, 11-16. *Rhombopora lepidodendroides* MEEK.
1, Longitudinal section of GE18(8) (m 1/3) (float)-p-PC-6101, showing overgrowth; 2, "typical" tangential section as shown by GE13E-bsf-PR-6101; 3, tangential section of PT16D(float)-p-PC-6101, showing modest difference between megacanthopores and micracanthopores; 4, tangential section of CH19A-p64-PC-5003, showing megacanthopores and micracanthopores of same size; 5, tangential section of MS06E (float)-p-PC-6101, showing extreme contrast between acanthopore sizes; 6, ×56, detail of diaphragm and basal lamina in longitudinal section of MS06E (float)-p-PC-6102; 7, longitudinal view of growth tip of GE01Da (float)-pAug-PC-4024; 8, transverse section, showing overgrowth, of GE13E-bsf-PR-6101; 11, ×90, detail of acanthopores and mesopores in tangential section of CH16F(m 1/3)-bfN-PR; 12, ×90, acanthopore in transverse section of PT12A (base), (float)-p-PC-6101; 13, longitudinal view of growth tip of CH22I-K (float)-p-PC-6101; 14, same view as in Figure 6; 15, longitudinal section, showing hemiseptum-like projection, of GE13L-p-PC-4001; 16, tangential section of RY02C(m 1/3)-bfN-PR-6101, showing circular zooecial openings and nearly equally sized megacanthopores and micracanthopores.

9. *Syringoclemis wrefordensis* NEWTON, n. sp., ×34, a longitudinal section of paratype WA08Be(u 1/2)-bfN-PC-6101, illustrating depth of mesopores.

10. *Leioclema* sp. from the Dillsboro Formation (Upper Ordovician) at Madison, Indiana, showing a typical tabulated trepostome mesopore.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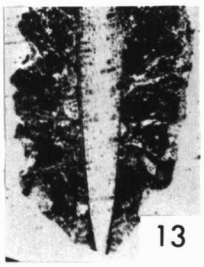
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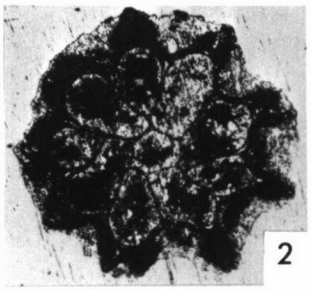
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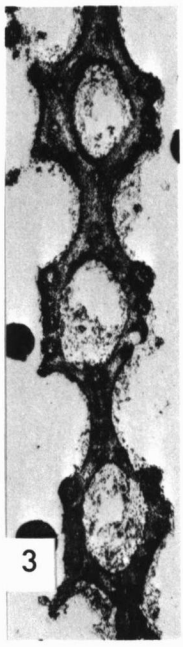
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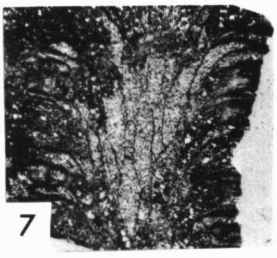
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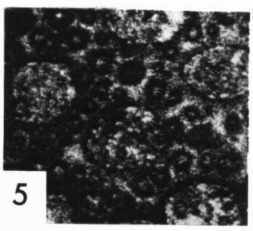
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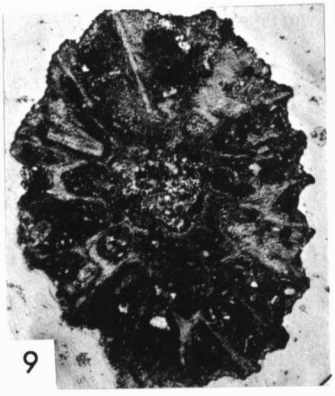
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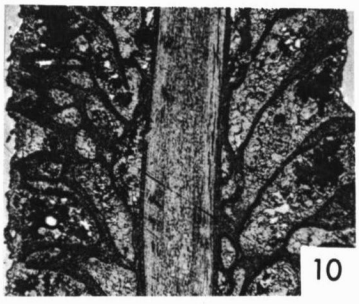
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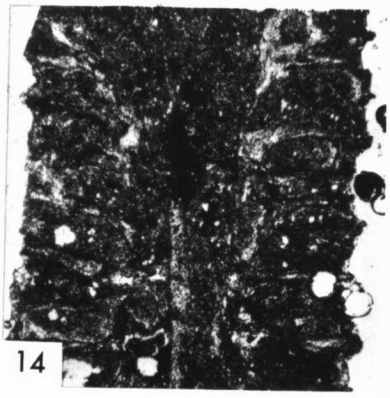
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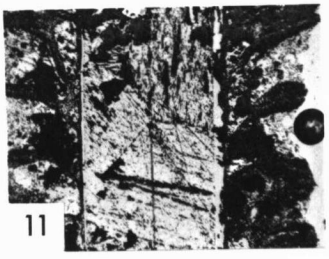
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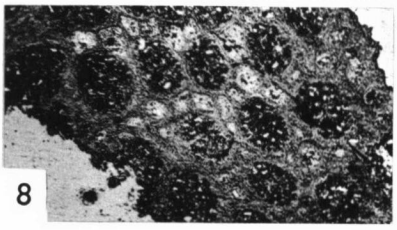
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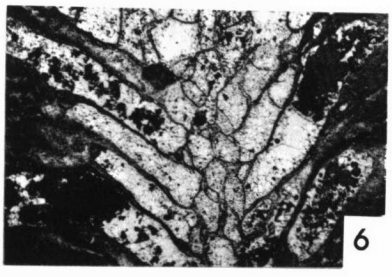
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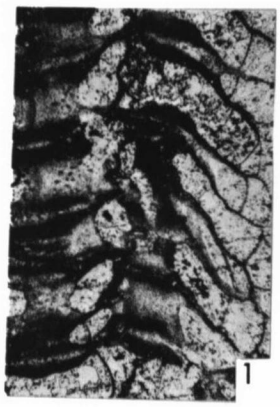
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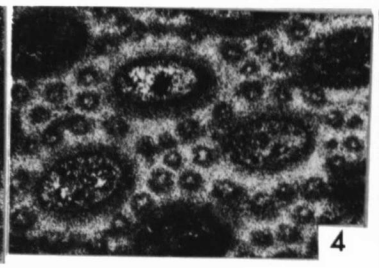
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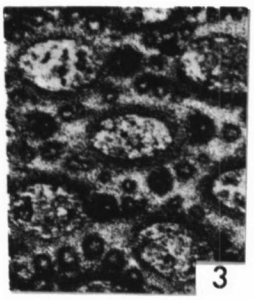
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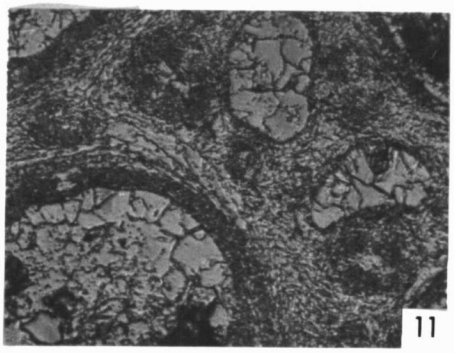
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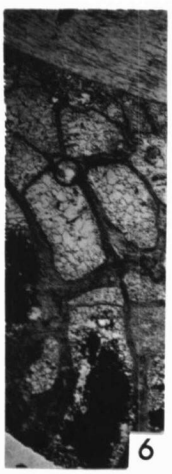
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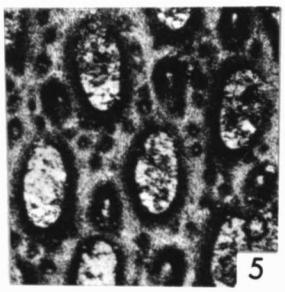
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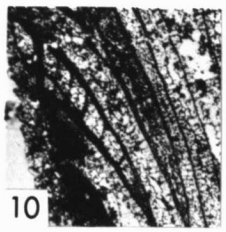
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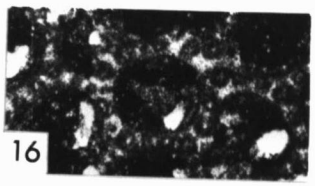
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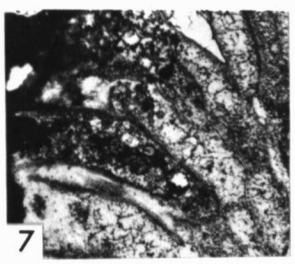
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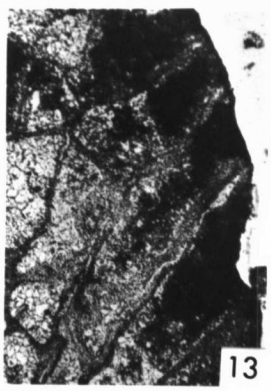
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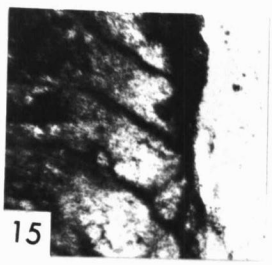
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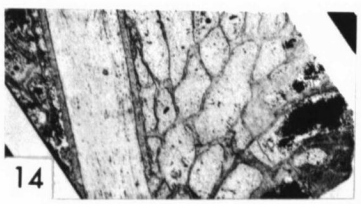
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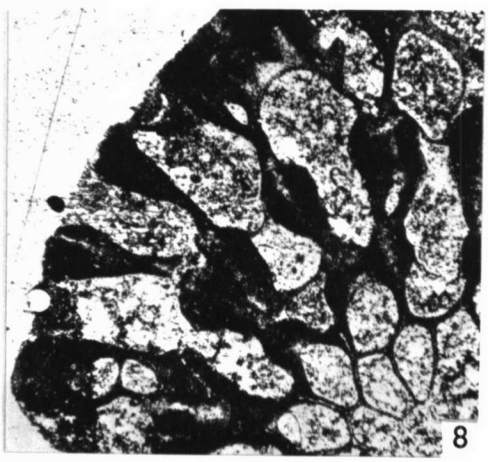
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